

ROGER SAGES

PERCEPTUAL DETERMINANTS OF
CHOICE BEHAVIOUR. A COMPARATIVE
ANALYSIS OF THE SYSTEMS UNDERLYING
PREFERENCES IN THE NEONATAL CHICKS

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TO STRAIGHTEN THE
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To

my parents



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This summary is based on five reports, referred to in the following as I, II, III and IV-V. The reports are:

- I. Sages, R. & Nyström, M. Perceptual Determinants of Choice Behaviour in Neonatal Chicks. I. Effects of Change and Dependence on Contrast and Colour of Shelter objects. Psychological Research Bulletin, Lund University, 1978, 18, No. 3.
- II. Sages, R. Perceptual Determinants of Choice Behaviour in Neonatal Chicks. II. Interaction of Figure and Background Colour in Pecking Behaviour. Psychological Research Bulletin, Lund University, 1979, 19, No. 5.
- III. Sages, R. Perceptual Determinants of Choice Behaviour in Neonatal Chicks. III. Maturationa1 and Situational Variables in the Early Development of Pecking Behaviour. Psychological Research Bulletin, Lund University, 20, No. 1.
- IV-V. Sages, R. Perceptual Determinants of Choice Behaviour in Neonatal Chicks. IV-V. Following Behaviour and Maturationa1 and Situational Variables affecting their Early Development. Psychological Research Bulletin, Lund University, 22, No. 2-3.

B a c k g r o u n d

Ethological research, after having concentrated on the analysis and description of species-specific forms of behaviour, has in part turned to the consideration of the perceptual aspects of the interactions between the individual and its environment, part of which falls under the concept of "innate releaser". Originally, this concept implies an innate perceptual preference governing a specific response mediated by central processes (Hailman, 1967; Lorenz, 1950; Tinbergen, 1948; Tinbergen, 1951). The term "innate" denotes the fact that the neuromotor structures which underlie the movement develop in a process of self-differentiation, guided by developmental instructions in the genotype. This characterization by I. Eibl-Eibesfeldt (1970), although concerning the so-called innate motor patterns, can be accepted in its main lines as valid also for the innate releasers, according to classical ethological thinking.

The concept of "innate releaser" implies that the releasing part of a stimu-

lus complex has developed in correlation with the activated behaviour under specific selection pressure. It also implies the existence of an innate releasing mechanism programmed to select the appropriate parts of the environmental situation and to release the appropriate behaviour. This has led to the problem of investigating exactly what aspects of a releasing stimulus situation are inborn, that is, genetically programmed. This means that these aspects will show up as specific preferences independently of the types of experiences, within broad limits, undergone by the animal prior to testing (Lorenz, 1965; Thorpe, 1963). This is the strong interpretation of "... genetically programmed". The weaker interpretation implies an interaction of the inborn components with experiential variables within certain limits, the observed preferences being then the result of this interaction (Kovach, 1971a, 1971b, 1978). "Unlearned preference play a significant role in behavioural development by providing initial differentiations in the effects of experience" write Kovach & Hickox (1971), working with approach behaviour in chicks elicited by different colours. Zolman & Lattin (1972), also working with approach behaviour to different degrees of brightness concluded to an interactive effect of genetical factors with environmental variables, against extreme maturational or environmental forms of explanation, as those advocated by Kuo (1932) or Bateson (1966). Similar conclusions were reached by Salzen, Lily & McKeown (1971) and Goodwin & Hess (1969).

An "innate releaser" is by definition restricted to a specific behavioural domain. Each different type of behaviour which has evolved as a result of natural selection must have its own specific releaser as a result of a parallel evolutionary development at the perceptual side, which it cannot share with another behaviour.

Colour can serve well to illustrate the problems generated by the above mentioned restriction on an innate releaser to function for only one specific type of behaviour. Any particular colour can appear in different stimulus situations for different types of behaviour. In the case of the same colour appearing in several stimulus complexes, we have then at least that part of the stimulus common to different behaviours and thence potentially to different innate releasers.

This possibility generates two questions. First, does colour preference as such have a genetically programmed basis independent of the other aspects of the stimulus complex? Or does it have its meaning only as part of a more complex total of perceptual determinants?

The works of Kovach and his co-workers on the colour preferences of the Japanese Quail seem to speak strongly in favour of the first hypothesis. Lines based on different colour preferences were easily obtained by genetical selection. The colour preferences were also shown to be true qualitative preferences and not the results of intensity preferences (Kovach, 1977). Similar results were obtained by Hurnik (1971) with the domestic chick. The same conclusion was reached by Fischer (1974) on the domestic chick, Fischer & Davis (1981) on both wild and selected breeds of the domestic chick, and by Oppenheim (1968) again on both wild and domestic breeds of duck. According to Kovach (1980), colour preferences in quail chicks are controlled by 4 to 8 Mendelian units of inheritance.

Also, the process involved in colour preferences is central and not peripheral. This has been shown by several researchers working with different species. The peripheral mediation of avian colour vision advocated and based on the supposed effect of retinal oil droplets, by several researchers (Hailman, 1964; 1967; King-Smith, 1969; Peiponen, 1964) has been severely criticised and shown untenable by Oppenheim (1968) working with duck, and Kovach, Wilson & O'Connor (1976) working with the Japanese quail. Working with cerebral lesion techniques, Salzen, Williamson & Parker (1980) have shown the existence of an innate neural system mediating specific visual discriminatory response tendencies and working independently of the neural pathways involved in imprinting.

Still, considering that the work of Kovach has been done exclusively with approach behaviour and that the phenomenal aspects of colour as object or background colour have not received any systematic treatment, the above conclusions cannot be accepted as valid unconditionally. Impekoven (1969) found white to be more preferred on darker backgrounds, Zolman (1969) found yellow more preferred than red or blue when exposed as background colour and the reverse when exposed as object colour. Dawkins (1971a; 1971b)

found the relationships between object and background colour important in determining the choices of the domestic chicks. Weidmann (1961) found differential preferences for white and black depending on the brightness of the background in gulls. Hailman (1966) found a mirror-image relationship between object colour and background colour with gulls. All these results imply that the second hypothesis stated above, that is, differential meanings for colour depending on the total stimulus complex cannot be ruled out. There is then the need to analyse more systematically the possible differential reactions to colour depending on its presentation as object or background colour.

The second main question can be stated as follows. Does the same colour generate identical responses in different functional domains of behaviour or can we expect reactions to colour varying differentially with different behaviours? The results obtained by researchers working with this problem are not clear-cut. Schaefer & Hess (1959), in the first study on this question found a mirror-image relationship between pecking colour preferences and approach preferences in the domestic chick. However, Mayer & Hailman (1976) were unable to replicate this result.

Davis & Fischer (1978) came to the conclusion that colour pecking and approach preferences are fundamentally the same in the domestic chick and interpreted their earlier opposite results (Fischer et al. 1975a, 1975b) as due to cold stress which reversed the chick's preference order. Hence here too, there is the need to continue studying the reaction to colours on different behaviours.

The concept of "imprinting" stands in a kind of complementary relationship to the concept of "innate releaser". To put it in the words of I. Eibl-Eibesfeldt (1970). "... object imprinting takes place when the object of an instinctive action shows a lack of releasing signals. If clear species-specific releasing signals are present, there is then no necessity for and an impossibility of imprinting". In most cases, however, the behaviour falls in between the two extremes of being completely genetically programmed or totally controlled by learning variables. Lorenz (1937) wrote of an "interaction between innate perceptory patterns and imprinting" and also; "one

might say metaphorically that imprinting fills out the spaces left vacant in the picture of the proper species, outlined in the bird's perceptory world by the data given by innate receptory patterns". Later, (1957) he spoke of the "mosaic" and the "regulative" types of species, the latter one being determined to varying degrees by sensory experience. Even here, the animal may be imprinted only to the characteristics for which he is programmed and needs a certain amount of exposure for them to acquire functional value (Kilham, Klopfer & Oelke, 1968).

So, even here, a genetically given tendency needs the cooperation of one or more experiential factors to produce the end result, that is the observed behaviour. A good example of this inborn-learned interaction can be found in the pioneering paper published in 1950 by Tinbergen and Perdeck. The aim was to ascertain the importance and possible inborn aspect of the red patch on the bill of the sea gull (*Larus Argentatus*). Their positive answer to the second of these questions was later modified in the light of results obtained by Nyström (1970), showing the preference for the red colour being admittedly inborn but second in strength to a preference for blue. This example is a good illustration of the intimate interaction between inborn aspects and environmental influences in the development of stable preferences, since the dominance of red over blue was shown by Nyström (1970) to result from an early period of conditioning occurring immediately after hatching. Such a period would occur normally in the natural environment of the newly hatched gull chick.

A study by Herbert & Sluckin (1969) shows not only the interaction between inborn factors and experiential variables but also the potential importance of interactions between two or more of these experiential variables. Pre-exposure to colour shifted the chick's preferences towards the exposed colour if exposed at optimal temperature (32°C) but exposure to the less preferred colour at a non-optimally low temperature (16°C) resulted in a shift away from the exposed colour.

Experiential variables are not restricted to post-hatching factors. Pre-hatching conditions have in some cases been shown to affect the colour preferences of the chicks, although results are not wholly consistent.

Exposure of eggs to green coloured light after the 18th day of incubation was shown by Wada, Goto, Nishigama & Nobukuni (1979) to reverse the natural preference for red over green in the domestic chick. But neither Oppenheim (1968) with gulls, nor Fischer, Davis & Nord (1975) with chicks could find an effect of pre-hatch exposure to coloured light.

Finally, Gunther & Jones (1963) found that non-optimally high incubation temperature during the first three days totally reversed the preference order for colour of the domestic chick.

Our work had three goals. To look for the potentially different stimulus value of colour depending on its appearance as object or background colour. To look for the potentially different value of colour for different types of behaviour. And finally, to look for the potential effects of imprinting in interaction with each of these two different situations.

M e t h o d

The research was made according to the following points.

a. Three behaviours were selected: shelter-seeking, following and pecking. Although differing from each other in many respects, they all have in common the figure - ground relation, that is, the search for an object visible by necessity against a background.

b. Two dimensions of stimulation were selected: colour with two instances, red and green, and figure-ground with two instances; object contrasting in colour and object not contrasting in colour against the background. This procedure allowed colour preferences to be determined as object or background colour preferences and so to allow a comparison between these two aspects. Also the chick's responses to the contrasting or non-contrasting aspect of the stimulus would be obtained.

c. Colour preferences were determined as early as possible post-hatching by testing dark-reared chicks. In this way it was believed that the results would be as near any potentially inborn preference as can be experimentally determined. Hinde (1966) has objected that one can never raise an animal

without experience. We adopt here the position exposed in Eibl-Eibesfeldt (1970) answer that this objection misses the point and that the only thing to be asked from a design is that it be at the appropriate level.

d. (b) and (c) taken together would give an integrated picture of the initial preferences of the chick for all aspects of the stimulus situation.

e. According to Parker (1929), Romanoff (1944) and Hogan (1973) the yolk sack present at hatching time provides the chick with sufficient nutrition to make ingestion of food or water unnecessary during the first days. Half of the yolk sack is absorbed after about 60hr post hatching and all of it after 6 days. This made possible the determination of the development of the initial preferences during the first three days without the interference of food or water. The aim was to look for potential modifications of the initial preferences by developmental variables. Three conditions were used: a) different periods of dark-rearing prior to testing; b) different periods of light-rearing in uncoloured pens prior to testing; c) pre-exposure to coloured objects or backgrounds during different time periods prior to testing.

f. It was expected that this final condition would be the more probable one to modify initial preferences as, reasonably, an exposure to a specific stimulus especially during the so-called critical period for imprinting (Hess, 1956; Kovach, 1970), should be a stronger factor than the simple presence or absence of light during a specific period.

Also, exposure to the object should probably have a stronger effect than exposure to the background, as evidently, a behaviour is directed towards its object and not towards the background on which the object stands.

g. Thus, the question of: 1) one system only lying behind the chick's preferences across several behaviours; or 2) one system lying separately behind one behaviour only or; 3) the existence even of at least partly separate systems for object or background colour preferences differentially for each behaviour or across all three behaviours, would hopefully obtain an answer.

Results

A- "Shelter-seeking" behaviour

The first paper (I) analyses "shelter-seeking" behaviour. In pilot studies, it was observed that most chicks showed a tendency to avoid staying in open fields and preferred to stay crouching near the walls of the pen, confirming observations made by Fabricius (1961) who considers this as a kind of filial behaviour in that it shows a striving by the animal to be under or near the parent. Hess (1959) observed the tendency to crawl under cover of a stimulus object even before the start of locomotion. Clements & Lien (1975) made similar observations when studying the effects of tactile stimulation on the initiation and maintenance of the following response in the Japanese quail. Due to these reasons, the behaviour was called "shelter-seeking".

A situation with two diametrically opposed cylindrical objects placed against the walls of a circular pen was designed. It was expected so that the chicks would choose them to stay nearby due to the tendency referred to above. Hence, by varying appropriately the stimulus characteristics of the object, a measure of preference could be obtained.

Previous researches have shown red to be one of the most preferred colours and green the least preferred one in several domains of behaviour. (Hess, 1956; Gray, 1961; Gunther & Jones, 1963; Smith & Bird, 1964; Smith & Meyer, 1965; Taylor, Hewitt & Sluckin, 1968; Dawkins, 1969; Herbert & Sluckin, 1969; Berryman, Fullerton & Sluckin, 1971; Kovach, 1971a; Kovach, 1971b; Salzen, Lily & McKeown, 1971; Fischer, 1974; Rodewald, 1974; Wada, Goto, Nishigama & Nobukuni, 1979; Salzen, Williamson & Parker, 1980; Fischer & Davis, 1981).

Also, the increased figure-ground effect resulting from brightness or colour contrast or more structured forms (a circle with tags as against a circle without tags) has been shown to increase the preference of chicks in various behaviours (Goodwin & Hess, 1969; Impekoven, 1969; Dawkins, 1971a; Salzen, Lily & McKeown, 1971).

Based on these two sets of facts, the first aim was defined as the study of the potential interaction between these two dimensions of stimulation.

Using only red and green as colours and having both the objects and the lining of the pen coloured allowed the presentation of objects of different colours (red or green) against a uniformly coloured background (red or green), making in this way only one object to contrast in colour with the background.

The results gave a clear preference for red over green, in accordance with the above-mentioned researches. But this preference for the red object was obtained only when it contrasted against the green background. When the background was red, the green object was preferred, that is, the one contrasting in colour with the background, albeit this preference being much less than in the previous case.

That can only be interpreted as meaning that, although there seems to exist a true preference for red over green as object colour, the choice of the chick will not be based only on the colour of the object towards which the behaviour is directed but will depend first on the more general structural aspect of the figure-ground relationship. Also, the preference for the contrasting aspect of the stimulation is stronger than the preference for object colour.

These results cast a serious doubt on all studies pertaining to determine the colour preference of different species. The results, whatever they are, must always be interpreted as possibly strongly dependent on the particular circumstances of the testing situations besides the colour aspect of the stimulus. This also, means that even when, under special conditions, true colour preferences can be ascertained, it can still be very difficult to draw conclusions on this basis about the functional importance of these preferences for the chick's behaviour under different conditions.

Also, the results are in favour of the second hypothesis stated above, that is, that the functional meaning of colour as a releaser is dependent on the total stimulus situation.

The development of the choice preferences observed on the same individuals over the three days period confirms this analysis. There is an increase in

the preference for the red object contrasting in colour with the green background during the three days period during which the chicks were observed. On the other side, the preference for the green object contrasting with the red background does not augment markedly and remains slightly above 50%. Hence, the relative strength of the contrasting and colour aspects of the stimulus remain unchanged. This is interesting for two reasons, as the contrasting aspect can be interpreted as the stimulus component releasing the chick's approach behaviour. Once near the object, (chicks choosing one object have a tendency to spend much longer time near it than in the middle parts of the pen) classical learning theory would predict an increasing preference for it as compared with the lesser chosen object, due to the association between it and the positively valued contrasting aspect of the stimulus. Also, since the chick evidently prefers staying near it, a reinforcement component should also be present.

Familiarity per se has been considered by Marx et al. (1963) a sufficient condition for a stimulus to become reinforcing. Guthrie's learning theory postulates the formation of an association on the sole basis of continuity, without the need for reinforcement. Considering that shelter-seeking is an emotionally laden behaviour, our results are also against Moltz (1960) theorizing on a quick conditioning to an emotionally laden stimulus. In a study on the colour preferences of chicks, Taylor, Sluckin & Hewitt (1969) found perceptual exposure as efficient as conditioning procedures in changing approach preferences. Hence, our results are also against this possibility.

Also, imprinting theory would lead us to expect an imprinting to the more often chosen object as exposure to it begins at a period considered optimal for imprinting.

Brown (1975) has shown that environmental imprinting can begin as early as 4 hr. post-hatching. Although this could account for the observations on the red object contrasting against the background (an increase in preference), as also the "learning" interpretation could account for, it can, as we have seen not account for the results on the green object contrasting against the background as no increase is observed here. But, as yet, this could be

interpreted only as a form of weaker imprinting to a stimulus less suited for that. The next part of the study can help to resolve this ambiguity.

Some chicks were exposed to backgrounds of the opposite colour for one or two of the days following the measurement of their initial preferences, inverting in this way the contrast relations. The observations point to the following. The preference for the red object, developed with groups having initially the green background, remains stable over the changes. However, an interesting phenomenon arises. Although the red object is still more preferred, the chicks oscillate much more often between it and the now contrasting green object, relative to what they did previously to the change in background colour. Hence, even if we could speak here of learning or imprinting accounting for the red preference, it is not so strong as to overrule totally the preference for the contrasting dimension.

But the behaviour of the chicks changing from red to green background rules out totally an interpretation in terms of learning or imprinting processes. Most of them choose directly the red object now in colour contrast against the green background. This shows clearly that no learning or imprinting has occurred to the green object during the period previous to the change of background colour.

This interpretation is strengthened by the fact that the amount of oscillations between the two objects is almost halved after the background change. That means that the now non-contrasting green object had not acquired previously any positive value.

B- Pecking behaviour

The second and third papers analyse pecking behaviour. The stimuli consisted of red, green or white dyed rice grains exposed on red, green or black background papers placed on the floor of the testing pens. As with the previous study, the chicks were confronted with two stimulus combinations, each one occupying half of the pen. Franck (1966), Dawkins (1969), Nyström (1972) and Sluckin (1965) have pointed to the superiority of a simultaneous choice situation over a successive one for revealing preferences. Also, to put it in the words of Nyström (1972), "... choice situations have clearest validity

for the initial pecking responses, since the newly hatched chick must at the beginning select those stimuli in its surroundings which are relevant."

There are some important differences between these two papers and the previous one. The particularities are best understood by a reading of the corresponding designs. The principal reason behind the modifications was to try to secure a gain in accuracy as regards the measurement of preferences after varying amounts of time post-hatching and/or varying schedules of pre-exposure before testing.

The observations gave clear-cut but totally unexpected results. Instead of the expected preferences for red and contrasting aspects, the results pointed unequivocally to the exact opposite, that is, a preference for green and non-contrasting aspects of the stimulus. Background colour per se does not seem to be important in directing the choices. Green was only slightly preferred to red, if at all. A reasoning along the lines of evolution theory would lead us to expect a clear preference for a green background as it is the colour that is most probable as background colour in a natural environment (Kovach, 1971a). On the other hand, the brightness of the background has a decisive effect on colour preferences for rice grains. Green dyed grains are significantly less preferred over red ones, when exposed on a white background. The reverse is obtained with grains exposed on a black background.

So far, our results are in support of the second hypothesis as here the functional meaning of colour is dependent on the other components of the stimulus situation.

We now look at the parts of the results which were the least expected. Both one-choice and two-choice testings indicate that pecking objects contrasting in colour against the background are less preferred than those of the same colour as the background. Furthermore, in each category, the combination with green-coloured grain was favoured over the combination with the red coloured grain as object. Taken together, the results point to a dominance of the non-contrasting aspect and of the green object colour in directing the choice behaviour of the chicks, the later aspect being controlled by the

former. As far as we know, the only similar result obtained previously was by Oppenheim (1968) where a green object on a green background was preferred to a green one on a grey background. But this study was made with ducklings, the natural preference of which is for the green colour, which is not the case with the domestic chick according to previous researches, as stated above.

Again, the results are in favour of the second hypothesis, with the green colour as object colour being the most preferred one but where the contrast-non-contrast dimension plays a major role in controlling the choice behaviour.

The observations reported in the third paper (III) concern the developmental aspects of the initial preferences, during the three days period under which observations were made. Time and exposure to light are revealed as the two controlling factors for the importance of background brightness in determining the choice of colour of pecking object. 48 hours rearing in the dark prior to testing result in the vanishing of the preference for green on a black background, whereas the chicks still prefer the red coloured rice exposed on a white background. So, the factor of time only has the effect of partly altering the dependency of choices on background brightness. But 48 hours of exposure to light before testing totally reverses the preferences relations on the black background, the chicks showing now a preference for the red object like those choosing object colour on a white background.

The modifications of choices due to time and light exposure are the same as regards the preferences for combinations of coloured objects and backgrounds. That is, the preferences after 48 hours of exposure to light are based on the same dimensions as previously (colour and object/background relation) but on opposite values of them. The red object colour is now the strongest controlling factor, making both combinations with red coloured objects to be favoured over the other two with green objects. Contrast still is important in determining choice behaviour, as for each of the two combinations with the same object colour, the contrasting one is preferred over the other one. Kovach (1977) observed with quail chicks a change from a strong prefer-

ence for blue over red at 7 hours post-hatching to a weak preference for red over blue at 47 hours, but this change occurred with the chicks kept in darkness prior to testing. Also, Menzdorff (1975) reports a change from a preference for red over green in the young of the Rock partridge to a preference for green over red in the adult. These two observations are, to our knowledge, the only ones which show a similarity to our results.

A strange aspect of the observations can be mentioned here, although the amount of evidence for it being scanty, it can be looked at as yet only very tentatively. A closer look at the results (III, Table 4) seems to indicate that the reversal of preference order for colour occurs earlier than for the contrast-non-contrast dimension. The reversal occurs then first with colour, red beginning to be preferred over green as object colour whereas the non-contrasting aspect of the stimulus is still more valued than the contrasting one. This could be interpreted as a sign of increasing importance in attention for the object of the choice behaviour, which is of course the rice grains and not the background.

A series of experiments were made with the aim of analysing the effects of different forms of pre-exposure prior to testing. Coloured pecking objects, backgrounds or both together were presented to different groups of chicks for varying durations prior to testing for choices preferences. Two clear results were obtained, the first being that pre-exposure influences the developmental course of preferences towards the exposed stimulus with all the three forms of exposure, but only with the longer exposure times. The second is that only pre-exposure to the green object on the red background is effective in reversing the final preference for red on a green background. All the other types are ineffective, in the sense that at three days post-hatching, the combination of red object on green background is so strong a stimulus as to be resistant to even 48 hours of exposure to the other combinations, with the above mentioned exception.

C- Following behaviour

Paper IV-V analyses following behaviour. The stimulus consisted of red, green, white or black painted moving cylinders exposed on red, green, white or black cardboard papers. As previously, the chicks were offered a two-

choice situation. The details of the design can be studied in (IV-V).

The one clear-cut result about preference for background colour is that initially, its value is intricately dependent on the brightness value of the moving object. The black object on green background and the white object on red background combinations elicit the strongest choices. We have here a situation similar to the equivalent one with pecking, where the brightness of one part of the total stimulus influences the preferences for the colour of the other part. As regards preference for object colour when exposed against uncoloured backgrounds, the observations point to the reverse conclusion. Preference for object colour is to a high degree independent of the brightness value of the background in controlling choice behaviour. Also, red is clearly superior to green in eliciting approach and following. The fact that dependence on brightness of the other part of the stimulus plays a role in pecking and in background but not object colour preference in following points to a central rather than a peripheral process lying behind and controlling the different choice behaviours.

Again we have here a support for the second hypothesis on a dependence of colour preference on the other parts of the stimulus. But also, concerning our second main question, we have evidence on differential colour preferences depending not only on the type of behaviour but also on different aspects of the stimulus for one behaviour, that is, both inter and intra behavioural variations.

All these results concern initial preferences of neonatal chicks aged six to 12 hours and kept in the dark prior to testing. And the observations have given clear-cut results (preference for red object colour over green independent of background brightness and interaction of background colour with object brightness) which should allow us to make predictions about the results to be expected in stimulus situations involving both object and background coloured. That means, the background colour should be less important in controlling choices than the red object colour. It is to be observed that, as yet, the data do not inform us on the potential importance of contrast.

The data obtained with both object and background coloured point in this direction. In situations involving two contrasting or two non-contrasting stimuli, the one with the red coloured object is always preferred to the one with the green coloured object.

But the results are less clear in situations offering choices between one contrasting and one non-contrasting stimulus combination. The differences are small, albeit in favour of the contrasting combination, independently of object colour. This shows that the contrasting aspect may be the controlling factor in determining the choices.

The data are not wholly consistent however, as we would, on the basis of the above reasoning and observations, have thought that the red object presented on a green background should be preferred to the red one on a red background. But the chicks strongly preferred the latter. The reason for this unexpected result is not evident to us.

On the whole we have here again a support for the second hypothesis and a radical difference in choice behaviour between pecking and following.

As regards the developmental aspects of the initial preferences, the brightness dependency of preferences of background colour is no longer evident after 48 hours exposure to the dark. All stimulus combinations are valued more or less equally. But exposure to light modifies the choices in favour of a strong preference for the red coloured background, independent of object brightness.

Exposure to light does not have a different effect compared with dark-rearing when the choice is of object colour exposed on white or black background. The preference for red remains as strong or becomes even stronger as compared to the one for the green colour. Similar results were obtained by Gray (1961), but Kovach (1971a) obtained no preference order with light-reared chicks on the fourth day post-hatching, although dark-reared chicks for the same duration had a clear preference for red over green.

These results together with those on the development of preferences for

background colour, should lead us to predict that red object and red background colour should be strong controlling factors in choice behaviour. Initially, there was also a preference for contrasting combinations. If this last preference remains stable during development, the results for choices of different combinations become more difficult to predict as all these three factors are not compatible in one stimulus combination for obvious reasons. For instance, it is not clear which of the following two combinations should be preferred if each stimulus factor adds up additively with the other and they are weighted more or less equally: green object on red background or red object on green background. Or this last one or red object on red background, as in each case, there are two of the three controlling factors. But one combination should clearly be the least preferred one according to the above reasoning and that is the one with a green object on a green background. That is also the only clear result obtained after both dark and light rearing for 48 hours. The other three combinations do not clearly differ from each other. The only strong preference was obtained after 48 hours light exposure in favour of the green object/red background combination when tested against the red object/red background combination. This is opposite to results obtained by Salzen et al. (1971), where chicks preferred different colours on different backgrounds with the exception of red which was always more preferred. Also, Boltz & Drickamer (1975) obtained the reverse preference order.

These results provide a very strong support for the second hypothesis, as otherwise any innate preference for a particular colour should have been present independently of the other aspects of the stimulus.

A series of experiments were conducted to analyse the potential effects of different forms of pre-exposure on the development of choice preferences. A moving coloured cylinder or a coloured background were used as exposure stimuli during different amounts of time. The results are clear-cut. Exposure to background colour did not have the slightest effect on the developing preferences. Neither exposure to the initially more preferred green helped to maintain this preference, nor did exposure to the after three days more preferred red help to increase the preference for combinations with red backgrounds. These results are totally opposite to those obtained

by Brown (1975) who concluded in favour of a very early imprinting to the background. Also, Kovach (1971) obtained an increase in approach following exposure to light. Taylor, Sluckin & Hewitt (1969) obtained a clear effect of background exposure in the direction of the exposed colour. According to Connolly (1968), the greater the perceptual exposure, the stronger should the neuronal model be, but our results point to a more specialized central process, working differently in different cases.

The situation is radically different for the effects of pre-exposure to object colour. Here the modifications are clearly due to an interaction between pre-exposure colour and testing combination. Two points are especially noteworthy. First, the green object on green background combination, which in all cases was clearly less preferred, becomes preferred over the other non-contrasting one after the two days of exposure. Its lesser value previous to pre-exposure can then not be interpreted solely in genetic terms. Secondly, the final status of the red object/green background combination in the preference hierarchy seems, at least if judged by the evidence collected here, not affected by pre-exposure to the red coloured object (which should favour it relatively to other test combinations); pre-exposure to the green object decreases the preference value of the red object/green background combination but do not make it clearly less preferred. Both Taylor, Sluckin & Hewitt (1969) and Gossop (1974) found exposure to a moving object a most potent stimulus in directing choices and clearly stronger than background exposure. That is exactly what we have found, but with the important restriction to the specific form of interaction between exposure colour and testing combination of stimuli.

Concluding remarks

An effort to integrate and interpret all the results obtained with the experiment series on shelter-seeking, pecking and following will be made here.

We begin by restating the two hypotheses formulated concerning the first main question. That is; does colour preference as such have a genetically programmed basis independent of the other aspects of the stimulus complex? Or does it have its meaning only as part of a more complex total of per-

ceptual determinants? Our results for all three behaviours point unequivocally towards an explanation in between these two statements. In all three cases, there are undoubtedly inborn preferences but again in all three cases, these preferences are modulated by at least some of the other aspects of the stimulus total. Also, preference for colour as background colour is not always identical to preference for colour as object colour and their interactions with the other parts of the stimulus follow different rules.

The second main question was stated as follows. Does the same colour generate identical responses in different functional domains of behaviour? Or shall we expect reactions to colour varying differentially with different behaviours? Our results point unequivocally towards the second statement. Not only does one colour generate different responses in different behaviours but also their interdependence on the other aspects of the stimulus follow different patterns in different behaviours.

As for the potential effects of imprinting, the results are negative for shelter-seeking. Only longer exposure time are effective and even then, not in all cases for pecking. And only object imprinting is effective in following behaviour. So here too, imprinting is differentially effective and this not only for different behaviours but also for different parts of the stimulus for one behaviour.

If we look at the results concerning the initial preferences, we see that the most marked differences are those between shelter-seeking and following, on the one side, and pecking on the other. Both the choices of colour and of contrast or non-contrast differ between them. This means that we have to do with at least two different systems, where the dimensions of stimulation are the same, but are reacted to in opposite ways, depending on which behaviour gets activated. Although functionally, all three behaviours are different, there are some similarities of both functional and physiological characteristics between shelter-seeking and following which differentiate them from pecking behaviour. From a physiological point of view, the chick does not need any food or water during the first three or four days of life, as its sustenance is obtained by the presence of the yolk sac. It has also been well documented that the pecking accuracy is very low on the first day, in-

creasing dramatically on the second and third days post-hatching. These first three days, by the way, happen to be the optimal ones for imprinting. Also, the amount of grains pecked and which are swallowed is very low on the first day and increases parallel with the accuracy of pecking (Spalding, 1873; Breed, 1911; Mosely, 1925; Bird, 1925, 1926, 1933; Cruze, 1935; Padilla, 1935; Hess, 1956; Hailman, 1967; Capreta, 1969). In short, the immediate survival value of pecking is low at the beginning.

On the other side, both shelter-seeking and following, although not fulfilling any immediate physiological needs with the exception of temperature regulation, as the thermoregulatory mechanism of the chick is inoperative until the seventh day (Gunther, 1964), are of evident survival value for the long-term adaptation of the chick to its immediate environment. It is important for the chick to be able to localize quickly a good shelter. It is also important for the chick to be able to follow efficiently the mother hen, as this will provide it with several important aspects of its environment, as shelter, optimal temperature and learning opportunities of the best objects to peck at. We can see here a reaction-chain: "following" → "shelter-seeking", "warmth" → "pecking-situation" (Vidal, 1971).

According to these arguments, the selection pressure should be strong for the development of an efficient and stable system of stimulus choice and preference. Such a system should contain the following characteristics.

1-An efficient mean of detection: it is obvious that contrasting aspects are much more effective in determining the localization of the stimulus than non-contrasting ones. A clear preference for contrast was also observed with both shelter-seeking and following behaviour.

2-A marked dominance of object characteristics over background: the "object" of behaviours like shelter-seeking or following is of course the object to seek shelter at or to follow. That implies that a change in background should not be allowed to disturb significantly the reactions towards the object, and so be given much less value relative to the object. With both shelter-seeking and following, the background as such was less important than the object. Also, as Stiles (1976) remarked, red is especially conspicuous against a background of sunlit green foliage.

3-A coordination of early preferences with some properties of the object best suited to initiate the response: the ancestral form of today's domestic hen has a red patch on the back of the head, serving then as a typical innate releaser. An inborn preference for red is then exactly what should be expected in relation with following. Although there is no similar information to our knowledge concerning shelter-seeking, the similarities between the two behaviours from a functional point of view makes a generalization of the above reasoning to shelter-seeking not too hazardous. Also, due to the above referred reaction-chain from following to shelter-seeking and as initially at least, the same object (the mother hen) will be optimal for both behaviours, the generalization of red preference from following to shelter-seeking is to be expected on the principle of "economy of means". Two dynamical systems with similar characteristics working together in close spatio-temporal relationship will tend to reduce to one system as a means of reducing energy expenses (Bruter, 1976).

An alternative explanation based, not on a positive preference for red, but on a negative preference for green, due to a natural selection pressure against favouring the background colour of the natural environment, can be considered less probable on the grounds that, first, non-preferred colours are not always aversive (Sahgal & Iversen, 1975) and secondly, green as background colour was in fact favoured over red initially.

4-The system should be structurally stable: in physical theory, a dynamic system is said to be structurally stable if reasonable amounts of variations in environmental conditions do not affect its efficient functioning (Bruter, 1974). The three properties listed above contribute to make the system controlling shelter-seeking and following structurally stable in this specific sense. Quite small variations in colour or brightness make a system based on non-contrasting aspects instable in the sense of introducing stimulus properties which transform it to contrast. The exact opposite is true of contrasting aspects of a stimulus, that is, even relatively large variations do not disturb its contrast character. The greater the structural stability of a system, the less it will be modifiable by environmental variations, and the better it will be in allowing for maximal functional effectivity.

5-The system should be relatively less open to changes due to environmental factors: Pre-exposure to background colour had no effect at all on the choice preferences of the chicks. Although pre-exposure to object colour was much more potent, it was evidently least effective against the "red object/green background" combination. This is logically the most interesting combination as it unites red object colour (see properties 2 & 3), contrast (see property 1) and a green coloured background which should be the most frequent in the natural environment of the chick.

It can be seen, then, that the initial preferences as recorded from our experiments correspond to the above listed properties of a stable and efficient system.

The results for pecking point to a radically different system. The differences do not lie only in other properties of stimulation being preferred but, more important, in the consequences that can tentatively be deduced from them. They can be best understood by making a point to point comparison with the five properties listed above in conjunction with following and shelter-seeking.

1-The early pecking preference favours non-contrasting stimuli. It is clear that this is the exact opposite of what we have called an effective mean of stimulus detection.

2-Although the green coloured object is preferred over the red one, it is partly controlled by the background brightness. So, compared to the results obtained with shelter-seeking and following, object dominance is less marked in initial pecking behaviour.

3-This point is more difficult to answer due to the following two reasons. First, colour and contrast are only two aspects of a stimulus. Form is another one which we have not studied here. A coordination of early preferences with some properties of the object best suited to initiate the pecking response could well be with only the form characteristics of the object of pecking. But several studies have shown colour to be the primary cue in eliciting choices, thus, making the above objection less probable (Marsh &

Walz, 1967; Berryman, Fullerton & Sluckin, 1971; Rodewald, 1974; Oppenheim, 1968; Kovach, 1978; Gaston, 1971; Stevens & De Bont, 1980). Secondly, there is no information comparable with the one about the red patch on the back of the hen's head. It could be that there are no such innate releasing stimulus coupled with pecking. Or it could be just the green colour as observed here. We have no means of deciding in favour of one of these alternatives. Concerning the green preference of the ducklings, Kear (1964) interpreted it as being only an evolutionary remnant from a period when green foliage served also as food for the young. Such a possibility could well offer an explanation in our case too.

4 & 5-From what has been said above, we see that the system controlling early pecking behaviour cannot be structurally stable. Small variations in colour or brightness will transform a non-contrasting stimulus combination into a contrasting and so less preferred one. Hence, such a system clearly lacks structural stability.

The prediction which could be made from these arguments is that such a structurally instable system should be modifiable by environmental factors to a much greater extent than a structurally stable one. The implications of this statement for learning opportunities during the first days post-hatching are obvious.

Physiologically, the capacity to peck develops earlier than the ability to follow. Also, it is well known that, in evolution, social behaviours are a later development than non social ones. Sluckin (1965) observed that newly hatched chicks peck at the object eliciting following and/or approach and spoke of a biological link between the two. Strobel & Macdonald (1974) observed that a foraging hen elicits approach and a pecking hen elicits pecking in its vicinity in neonatal chicks. Similar observations were made by Sherry (1977) on the young of the Burmese Red Junglefowl. That means that a pecking-inducer stimulus initiates and sustains behaviour not directed towards itself. The high motivation for pecking guarantees that enough pecking will be produced regularly without the need for food reinforcement during the early post-hatching days (Strobel & Macdonald, 1974; Hørlyk & Lind, 1978).

We can then speculatively interpret following and so imprinting to a moving object which it entails, as a means of regulation introduced to stabilize pecking behaviour. This implies two things. First, that the system controlling following be an efficient and structurally stable one to guarantee the quickest imprinting to the best suited object (the mother hen). And secondly, that the system controlling early pecking should not be stabilized strongly from the beginning to allow for the learning of the best pecking objects as a consequence of following and/or approaching the imprinting object. These two things are exactly what we have found.

The last part of the interpretation will be devoted to the presentation of a geometrical model for the development of pecking preferences. As will be remembered, there was a total inversion of choice preferences from the initial ones observed on the first day to the last ones observed on the third day post-hatching. The initial preferences were shown to make a structurally unstable system, whereas the last ones, favouring contrast and the red coloured object evidently form a structurally stable system. In physical theory, a structurally unstable system is considered unlikely to remain in that state but will, sooner or later, get modified towards a greater degree of structural stability (Bruter, 1974). The mathematical theory called Catastrophe Theory recently developed by Thom (1972) offers several geometrical models aimed at describing the sudden changes occurring in some developmental morphologies. By its very nature, it can be used to model situations of very different kinds, from physical to sociological ones, and has been used recently in productive ways by some researchers (Zeeman, 1977).

One main principle is the classification and description of forms obtained from the continuous variations in one or more controlling factors which at certain points in their variations lead to sudden changes in the behaviour they control. One of these models is the so-called Cusp of Whitney. It is obtained by variations of two factors controlling one behaviour variable. To apply it to our case we see that the behaviour variable is the choice preference of the chick, which undergoes a radical change as a result of increase in two controlling factors, which are post-hatching time and amount of exposure to light. The cusp is presented in Figure 1.

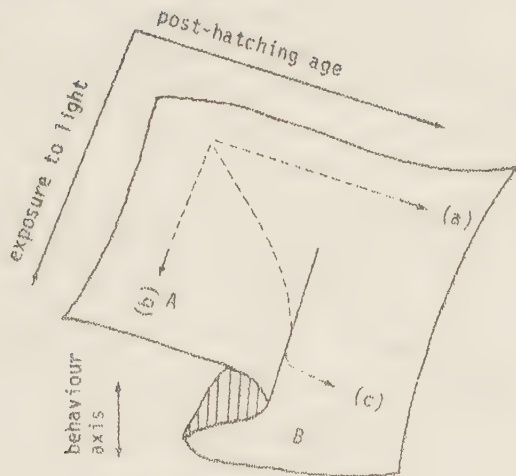


Figure 1. The Cust catastrophe model for the change in preference occurring in early pecking behaviour.

The part of the surface called "A" represents the choices of green and non-contrasting aspects, the part called "B", the choices of red and contrasting aspects. As can be seen from Figure 1, an increase in post-hatching age only (corresponding to our dark-reared chicks tested after varying amounts of time) will not lead to a radical change but only to small modifications (see line (a)). It is also exactly what we obtained as dark-reared chicks tested after 48 hours do show a preference hierarchy like the initial one, but less marked. Exposure to light confined to a small portion of post-hatching age will not transform the preferences either (see line (b)). But a simultaneous increase in both controlling factors will lead to a sudden jump from part "A" to part "B", that is, to an inverted preference hierarchy, which also will show much stronger structural stability.

In other words, in situations lacking a strong object to get imprinted at, the internal dynamics of the system controlling pecking behaviour will lead after some time of exposure to light (the chicks obviously live in light

and not in darkness) to a structurally stable system, offering in this way an effective instrument for a good adaptation to the environment. It is interesting to note in this connection that Rose et al. (1975), studying the biochemical changes occurring during imprinting in the domestic chick, observed a triggering effect of light stimulation on certain general cellular developmental events.

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*Perceptual Determinants of Choice Behaviour
in Neonatal Chicks*

*I. Effects of Change and Dependence on Contrast
and Colour of Shelter Objects*

by Roger Sages and Mats Nyström



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A b s t r a c t . - Studied the preference behaviour of 288 neonatal chicks (Cobb's race) in an experimental situation which offered a simultaneous choice between two coloured objects, one of them contrasting to the background colour. For two out of eight groups (N=80 in each), the background remained the same during the three days of the experiment. For the remaining six groups (N=16 to 24 in each), the background, and thus the colour contrast to the two objects, was changed between days. The results show that contrast was superior to the hue dimension in determining choices. Within the latter dimension preference was strong for the red object. Furthermore, the oscillation behaviour of the chicks between the two objects was tied to the condition of stimulation. However, figure-ground reversals, obtained through change in background colour, gave rise to marked changes in choice behaviour. The results were interpreted in terms of a three factor model in which not only the static features of the stimulation offered by both figure and background, but also the temporal ordering of the chick's choices (characterised here as "shelter-seeking") were taken into account.

It is generally believed that most species are particularly sensitive to stimulation during their neonatal period. Even a brief exposure is often sufficient to bring about marked changes in the behaviour of a young animal, changes variously referred to as perceptual learning, handling effects, or imprinting. However, such effects are frequently confounded with effects arising from uncontrolled sources of stimulation, i.e. other than those directly studied (Sluckin, 1973).

A weak design can, for example, involve stimulation in one setting, testing in another, and rearing in a third. Uncontrolled effects may also arise from differences in physical variables such as temperature and illumination which can occur during transport and care-taking activities.

Furthermore, it is frequently overlooked that the mere manipulation of parameter values may be a confounding factor. There is evidence that early preference behaviour in many cases could be

explained as perceptual reinforcement emerging from unintended quantitative changes in the level of visual stimulation (cf. Meyer and Auguston, 1969). Thus, Broom recorded a double reaction in young chicks to change in illumination level. The first was a general effect due to change per se. The second reaction was dependent on the context and was shown to be more pronounced after (i) long exposure periods, (ii) change from weaker to stronger stimulus and (iii) change from an indirect to a more direct source of stimulation (Broom, 1969). Thus, it seems that a chick which is only a few hours old is sufficiently mature physiologically to make very fine perceptual discriminations.

Young precocial birds are also known to develop unexpected "attachment" for static features of the pen in which they are reared. In this case the relative conspicuousness of wall texture seems to be the essential factor (Taylor et al., 1967). The behaviour is similar to imprinting, but so as to avoid overinterpretation it is perhaps best described as a kind of shelter-seeking within a deprived situation.

The purpose of the present experiment is to study how such preference behaviour develops in a well controlled situation where two shelter objects are continuously present. The stimulus properties employed are quality of contrast and object colour. The choice behaviour is studied during three days which makes it possible to measure the naive preference as well as its consolidation in a constant situation. For this purpose two larger groups receiving different contrast values are studied. Using the results from these groups as a base-line, the effects of change will be inferred from other groups receiving reversals of the figure-ground quality during the establishment of preference behaviour. It is theoretically important whether or not an imprinting-like behaviour could be reversed when preference has already developed.

Method

A total of 288 dark-hatched chicks belonging to Cobb's race were used. Beginning at the age of about 36 hours, each chick was housed in a circular pen, 38($\emptyset$) $\times$ 27(h) cm. The inside of the wall was completely covered by easily removable red and green sheets of paper (RB-3-16-28 and GY-6-8-16, respectively, according to Hesselgren's object colour standards¹). Two cylindrical objects, 9($\emptyset$) $\times$ 27(h) cm, were placed diametrically opposite to each other close to the wall inside each pen. One of these objects was covered with red, the other with green paper of the same kind as that used to line the walls of the pen with.

Thus, in each pen, one of the objects contrasted while the other was similar to the wall colour. The contrasting or non-contrasting character of the two objects could be inverted by changing the background colour from red to green or vice versa, offering a new choice situation in respect to the place as well as the figure-ground values involved. The chick's position relative to the objects was recorded seven times during a 90 min session, this being repeated three times, giving 21 observations a day.

The chicks were individually exposed to this binary choice situation for three consecutive days. Stimulation either remained the same or was inverted between days. Two groups (I and V) of 80 chicks each were constantly exposed to the green respective red background (cf. Fig. 1). Two other groups (II and VI) of 16 chicks each started with green respective red background but colour was inverted between day two and three. Similarly, two groups (III and VII) of 24 chicks each started as the latter groups but background colour was now changed between the first and second day. Finally, two groups (IV and VIII) of 24 chicks each began as the last groups with change in background colour

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between the first and second day but colour was changed back to the original hues between the second and third day.

Only a limited number of pens could be effectively observed each time so satisfactory sample size was obtained by several replications of the whole design. It may also be emphasized that the two shelter objects always remained the same for all eight groups. No food was offered since the nourishment provided by the yolk sac is sufficient to last the chick for the first three days after birth. Temperature was held constant at $+32^{\circ}$ C.

A n a l y s e s

The daily record of each subject consisted of a series of 21 binary preference scores towards either the contrasting (c) or non-contrasting (nc) shelter object. The distribution of the scores among these two categories was tested for each group and day using a two-tailed Wilcoxon test. The same test was also employed in testing for significant trends in the choice-distribution between days.

An alternative type of analysis was based on only those individuals which exhibited a significant daily preference score, according to a Binomial testing of their 21 c and nc scores. This more conservative preference measure, built on the proportion of determined c and nc individuals, was for example used in Table 1.

Finally, their daily sequence of 21 choices was analysed for length of runs of successive c and nc scores. The daily series of preference scores of one individual, say 15 c and 6 nc scores, could be obtained in everything from two to 13 runs. Using a special statistical procedure (Hollander and Wolfe, 1973), the most probable outcome could be calculated, in this case 10 runs. Thus, each sequence could be classified as having more or less runs than what could be expected

by chance. Further, a group of subjects could be classified as having many or few runs according to this criterium. This statistic permitted a comparison of the number of runs for different proportions of c and nc scores.

As a control for possible position effects, the tendency of the chicks to choose the one previously preferred out of the two shelter objects was examined after interchanging their positions. One group of twelve chicks was exposed to the two objects during two days but their positions were interchanged on the third day.

It was observed that most of the chicks showed a definite preference for staying near one of the objects and avoided the open field in the middle of the pen. Furthermore, chicks showing a clearcut preference for one of the objects followed that object to its new position. Before change, six chicks revealed a significant preference for the c-object. After change, in fact all these chicks followed the object to its new position. Thus, stimulus characteristics, and not position of the respective object, determined the direction of choices. This observation is also supported by earlier findings (Sages, 1973).

R e s u l t s

The object preference varied in a systematic way between the eight stimulus conditions. Starting on the first day, chicks living in a pen which had a green wall-lining (Fig. 1; group I) showed a significant preference for staying near to the contrasting red object. This preference increased on the second and third days. Preference for the contrasting object was only slight and did not increase between days in the groups continuously confronted with a red background (group V).

Experimental inversion of background colour caused significant deviations from this base-line behaviour. Change from green to red background as a rule resulted in significant decrease of

preference for the contrasting object, whereas the reverse was true for groups receiving change from red to green background (Cf. Fig. 1; groups II-IV and groups VI-VIII, resp.).

The more conservative calculation based on only those subjects which exhibited a significant daily preference score (cf. p.4) confirmed these trends in all details.

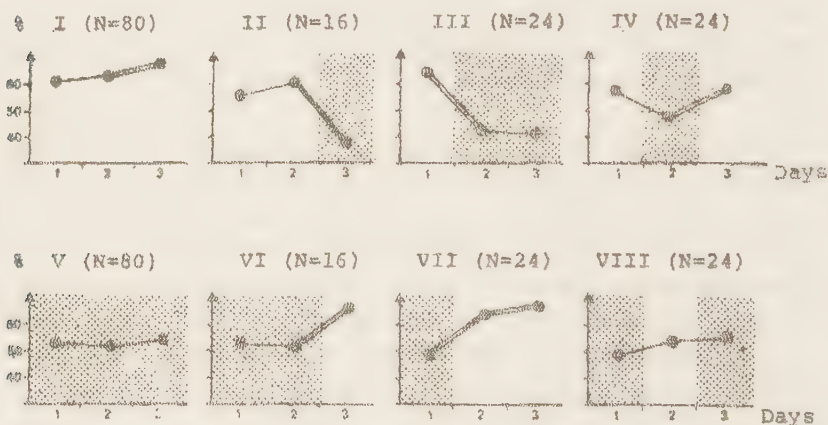


Fig. 1. Daily percentage of choices of the object contrasting to the green (empty field) or red background (hatched field). Heavy lines indicate significant changes in preference behaviour between successive days.

Data on the number of runs in the groups receiving change in background colour (groups II-IV and VI-VIII) reveal one general trend (see "Totals" in Table 1). Change of background colour from green to red was accompanied by an increase of runs, 20 percent of all replica having more runs than expected by chance before change has taken place, versus 52 percent after change. The opposite was evident for change in background colour from red to green since corresponding groups decreased from 27 to 14 percent.

These totals were further split up to show the proportion of choices for each of the four sub-groups having different choice pattern, i.e. choice of contrasting or non-contrasting object and significant or non-significant type of choice. Table 1 shows that the changes discussed above can be traced to two of these subgroups. Firstly, change from green to red background was accompanied by an increase in the number of runs of the subgroup having non-contrasting choices. Secondly, change from red to green was accompanied by a decrease in runs for the subgroups whose choice of contrast was significant.

Table 1. Proportions of test replica which reveal more runs than expected in the groups receiving change in background colour.

Initial colour	Direction and strength of choice	Pro-portion	New colour	Pro-portion	Difference P
Green	Contrast, sign.	3/6		2.5/4	
	Non-contrast, sign.	1/3		4/6	
	Contrast, n.s.	0/6	Red	0/6	
	Non-contrast, n.s.	0/5		5/6	
	Total	4/20 (20%)		11.5/22 (52%)	< .05
Red	Contrast sign.	3/4		1.5/6	
	Non-contrast, sign.	1/2		0/1	
	Contrast, n.s.	0/6	Green	0/6	
	Non-contrast, n.s.	1/6		1/4	
	Total	5/18 (27%)		2.5/17 (14%)	< .05

Discussion

In what follows three types of explanations are discussed. The first one only concerns the isolated preference value of the respective stimulus objects. The second includes, in addition, the relationship between the object and the background, whereas the third explanation also takes account of the temporal ordering of exposure qualities.

Several studies have found a more or less pronounced preference in young chicks for red hue and low preference for green (e.g. Smith and Bird, 1964; Salzen, Lily and McKeon, 1971; Hess, 1973). Various suggestions have been offered to account for this fact. According to Gray (1961), a red patch present on the body of the female ancestral form of domestic fowl (*Gallus bankiva*) could be interpreted as a specific releaser, in an ethological sense, whence a corresponding preference for red hue has developed in the chick. Thus, the observed preference should be regarded as an adaptation to a phylogenetically archaic situation.

Weak approach (preference) to green objects may be explained on the basis of another type of selection pressure. In the natural habitat of fowl there is green vegetation, movable foliage which the young chicks might confuse with the more important movements of the mother hen unless they had a low preference for approach to green objects (Kovach, 1971).

However, such analyses as the ones above are intricate and liable to lead to premature conclusions. In young Herring gulls, for example, "figure-ground features", as well as the interrelations of these, contribute in a complex way to the actual colour preference (Nyström, 1970). Thus, explanations based on isolated preference values appear incapable of elucidating our results with respect to combinations of object and background colours. As will be evident below the preference behaviour could not be interpreted by the aid of a one-dimensional concept.

Apparently, the contrast factor has been an important determinant of choices since the red object was preferred only when set in colour contrast to the green background. Further, green as an object colour, though of low preference value alone, was chosen more frequently when placed against a contrasting red background than against a green one. In this

situation it was even slightly more preferred than the red object colour.

Accordingly, we must assume that the preference of the chicks is determined by the joint effects of two positive factors, red object colour and contrast to the background. In groups receiving a red background, each of the two objects possesses one positive factor giving rise to a preference of medium strength.

The effect of change of background colour can now be interpreted as the joining of the two positive factors into one object (in case of change from red to green background) or as the separation of previously unified factors into two opposite objects (in case of change from green to red background).

The first situation, change to joint condition, results in an increase of the preference of the object possessing the two positive factors, i.e. the red object contrasting to the green background. The gain is greater after a long period of exposure to the "separate condition". Logically, a long exposure to the "joint condition", followed by a separation of the factors should give rise to a pronounced decrease of preference, a supposition which is not borne out (see below).

The joining or separation of attractive features may provide an explanation of the observed changes in the number of oscillations between the two objects. Generally, a decrease in preference of one object entails an increase in runs. This is a reasonable result when dividing the two positive factors into separate objects.

However, a weakness connected with this two-factor model is the preference of the chicks after change from green to red background colour. Contrary to the sustained low preference for the red object (less than 50%) in the group continuously receiving

red background (group V), the present groups (II-IV) show a high preference for the red object after change of background colour. According to the two-factor model we would expect a much lower percentage, about the same as in group V. This sustained high preference cannot be an effect of age or repeated presentations to the same stimulus. An interpretation in terms of classical conditioning would explain the effect as a result of pairing with the contrast factor which has a positive valence in all groups already from the beginning of the experiment. But even this interpretation is not sufficient to explain the results as a similar effect, related to the green object would occur for the chicks receiving a red background during all three days, and this is not the case.

We believe that a model proper should involve not only the figure and background features of the stimulus situation but also the temporal aspects of the chick's behaviour. In particular, an extension of the well-known ethological notion of behaviour, as divided into appetitive and consummatory parts, is relevant here. The observed shelter-seeking behaviour may, thus, be analysed into two consecutive parts: approach to the stimulus object, followed by the releasing of the specific part of behaviour, in this case staying near to the object. Correlatively, as already stated, the object releasing the whole sequence can be analysed into two components, its relationship to the background and its intrinsic colour quality.

This first one, the contrast quality, serves as a stimulus for approach, while the second one, the object colour, determines the duration and strength of the latter part of the sequence.

This third model explains the preference for contrasting objects, already evident from the beginning. It also explains the stronger preference for the contrasting red object al-

ready from the start. Finally, it would account for the sustained low preference for the red object in the groups with continuous red background, as well as the high preference for the same object colour in the groups changing to red background. Here, the chicks preferred and stayed near to the red object before change, and continued to do so after change of background colour. In this case the contrast quality of the opposite green object had some distant approach releasing effect, which explains the increase in the number of oscillations.

The present design permits further studies of other domains of behaviour using the same perceptual determinants as in this experiment. Hopefully, it will facilitate direct comparisons of the mechanisms directing choice behaviour in different functional contexts.

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PSYCHOLOGICAL RESEARCH BULLETIN

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*Perceptual Determinants of Choice Behaviour
in Neonatal Chicks*

*II. Interaction of Figure and Background
Colour in Pecking Behaviour*

by Roger Sages



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A b s t r a c t . - Studied the pecking behaviour of 450 neonatal chicks (Cobb's race) in an experimental setting which offered either a one-choice or a two-choice situation. The stimuli (white or dyed rice grains) were presented on white, black or coloured backgrounds. The aim was to analyse the relative preference value of red and green as figure and/or background colours. The results showed that non-contrasting relations were superior to contrasting ones in eliciting pecking responses. Also, the initial colour preferences of the neonatal chicks appeared to be wholly dependent upon the relationship between figure and background colours.

It is a general finding that many species of birds show a fixed preference order for different colours already from the first days of life. This fact has been seen by several writers as supporting an interpretation in terms of evolutionary selection mechanisms (Tinbergen & Perdeck, 1950; Hess, 1956; Gray, 1961; Lorenz, 1965; Kovach, 1971; 1974; Fischer, Morris & Ruhsam, 1974). Colour preferences have regularly been found to vary between species, lending further support to the phylogenetical theory. Red has been found to be the most preferred colour in domestic chicks of different breeds (Hess, 1956; Gray, 1961; Smith & Bird, 1964; Oppenheim, Jones & Gottlieb, 1970; Kovach, 1971; Saizen, Lily & McKeown, 1971). Green has in the same studies consistently been the least preferred colour. On the other hand, Hess (1956) and Oppenheim (1968) found green to be the most preferred colour in Peking ducklings, and this result holds also for the Japanese quail (Kovach, 1974). Kear (1964), Hailman (1969) and Nyström (1972) found preferences for blue and red in several species of gulls, with green as the colour eliciting least pecking. However, results regarding the domestic chick are ambiguous. Some investigators have found a bimodal preference, with pecks both at red and blue (Curtius, 1954; Hess, 1956). Others have found a bimodal preference for red and blue with dark-tested chicks and at violet and orange for chicks

tested in the light (Fischer, Morris & Ruhsam, 1974). These researchers used an apparatus that allowed for the projection of coloured light spots in a dark testing pen. Furthermore, Hess reported changing colour preferences in relation to seasonal variation. Recently, Machlis (1977) reported preference for green over red in an experiment involving pecking responses. The situation may be still more complicated as already indicated by Curtius (1954), who found bimodal preferences with black and unimodal preferences with white background.

One characteristic of all the above studies is that the phenomenal aspects of colour as figure or background colour seems to have received only little attention. In pecking experiments, backgrounds have usually been white, grey or black, with the exception of a study by Rodewald (1974), in which a preference of red over green or yellow background was found. However, these experiments had quite another aim and the chicks were always presented with white dots on coloured backgrounds.

The question could be asked, if within one and the same functional domain of behaviour, preference for one specific colour could be obtained irrespective of its presentation as figure or as background colour. And, correlatively, if the lack of a positive response to one colour will show under both types of presentations, i.e. a figure and as background. An alternative outcome would be that the more preferred figure colour turns out to be the least preferred as background colour, and vice versa.

This outcome would be predicted from an evolutionary point of view. Also, it would be theoretically profitable to analyse and compare colour preferences from different functional domains of behaviour, e.g. pecking, following, shelter-seeking. A similar study has been conducted in the species *Larus Argen-*

tatus by Baerends & Kruijt (1973), where different reactions by the birds to their eggs were analysed. The results showed that physically identical stimuli may be evaluated differently, according to the momentary activity in which they are involved. In a previous paper, dealing with shelter-seeking behaviour in chicks (Sages & Nyström, 1978), the authors analysed colour preferences and found that red as object colour was favoured over green when contrasting in colour against a green background. However, this preference was only slight at an early age (24-36 hours) and non-existent if the red object was shown against a red background. Furthermore, the order of presentation of the stimuli had differential effects.

Again, can we expect different preference orders based on different systems of choices for each one of these behaviour domains, or is there only one system directing choice behaviour in all cases? Research conducted under as similar experimental conditions as possible across several functional domains of behaviour could answer these questions more satisfactorily than ex post facto comparisons of results obtained by investigators under differing conditions.

The present paper aims to answer some of these questions by studying colour preferences in pecking behaviour. The importance of colour both as figure and as background colour will be analysed. Experimental manipulations after initial exposure will be considered later on and will appear in companion paper.

Method

Subjects.

During a period of several months a total of 450 chicks (*Gallus domesticus*, Cobb's race), were tested for their colour preferences. Hatching temperature was 37°C and relative humidity during hatching 85%. Chicks were aged about 6 to 12 hours at the time of testing.

Apparatus.

Plywood pens, 25 cm. high $\times$ 30 cm. long $\times$ 36 cm. wide, were placed pairwise on a plywood support in a metal frame as shown in Figure 1.

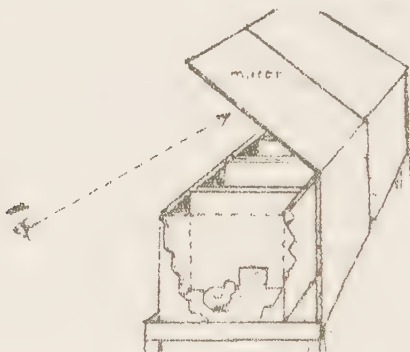


Fig. 1. The two testing stands with two double pens each.

A mirror placed above the pens allowed for observations during testing. Light was obtained by two 60W neon bulbs placed outside and above the short sides of the pens. Temperature in the test room was held constant at 28°C.

Stimulus material.

The stimulus material for the background consisted of coloured cardboard paper easily inserted under the pens on the plywood floor. The four colours used were red (RB-3-16-28), green (GY-6-8-16), black and white, according to Hasselgren's colour standards.^{1/} The material for the stimulus figure were ordinary, elongated rice grains, white or dyed red or green to match the cardboard colours, using commercial food colouring.

Procedure.

After hatching in a dark incubator, two chicks were placed in

^{1/}

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small, grey plastic pens in dark room. The number of chicks tested each week varied due to practical reasons. All handling of the animals was done in the dim light from an electric torch. At testing, the two chicks from each plastic pen were placed together in one of the test pens, four such pens being observed during each test session. Each pair of chicks was tested only once. The specific stimulus combinations were re-arranged in each pen before the introduction of the next pair of chicks. The design of the experiment is presented in Table 1.

Table 1. Number of pairs of chicks tested for different combinations of figure and background colours.

General type of combination				
Different figure colours against identical background colours	r/G, g/G	r/R, g/R	r/W, g/W	r/B, g/B
	N=8	N=8	N=8	N=8
Identical figure colours against different background colours	r/R, r/G	g/R, g/G	w/G	w/R
	N=8	N=8	N=31	N=26
Two different contrasting combinations	r/G, g/R			
	N=8			
Two different non-contrasting combinations	r/R, g/G			
	N=8			
All four possible combinations of red and green colours	r/R	g/G	r/G	g/R
	N=17	N=17	N=45	N=25

Combinations separated by a comma were presented simultaneously each one covering one half of the pen: the remaining ones were offered alone, covering the whole surface of floor of the pen. Small letters refer to figure colour and capital letter to background colour (r, R=red, g, G=green, w, W=white, B=black).

Observation technique and scoring.

Two different procedures were followed.

Procedure I. - Two pens at a time were observed for 15 seconds and the number of pecks to both kind of stimuli were registered and counted together for the two chicks in each pen. (All groups in Table 4). This procedure was repeated 12 times in succession. The sum of pecks over the 12 observation periods for each pair were calculated to form the score for them. Then, the chicks were removed, the pens cleaned, the stimulus material rearranged and new pairs of chicks introduced for testing.

Procedure II. - The groups tested in this procedure had only one combination of figure and colour background present, different groups getting different combinations (all groups in Table 2). Two scoring techniques were used in this procedure: (1) for the w/G and w/R groups the scoring technique was identical to the one described above in Procedure I. (2) For the g/G, g/R, r/R and r/G groups, an all-or-one method was used, scoring a "one" if at least one peck had been observed during each 15 seconds period, and a "zero" otherwise. 25 such observations were collected for each pair of chicks. The treatment was identical to the one for the other groups in all other aspects.

R e s u l t s

The data obtained under the conditions which only contained one object and one background colour are presented in Table 2. We can see that the difference in preference between white grains on red or green background is little. The order of preference for the last four combinations follows the arrangement of presentation in Table 2, viz. a preference for non-contrasting combinations over contrasting ones, and for green over red rice colour in each of these two cate-

gories. The probability values given below in Table 3 mainly confirm this description.

Table 2. Number of pecks given by chicks exposed to each of the six combinations of figure and background colours and obtained following Procedure II.

Groups	Sum.	M	N
w/G	253	8,43	31
w/R	195	7,50	26
g/G	160	9	17
r/R	135	6	17
g/R	127	5	25
r/G	169	3	45

The mean is given for groups w/G and w/R and the median for groups g/G, g/R, r/R, r/G. Small letters stand for figure colour and capital letters for background colour.

Table 3. Two-tailed significance levels for comparisons between the six groups from Table 2.

The Kruskal-Wallis Test.						
Groups:	g/G	g/R	r/R	r/G	P <.001.	
The Wilcoxon Rank Sum Test.						
Groups	P	Groups	P			
w/G	>.05	g/R	>.05			
w/R		r/G				
g/G	<.002	g/G	>.05			
g/R		r/R				
r/R	<.0001	g/G	<.00006			
r/G		r/G				
		r/R	<.05			
		g/R				

The results from the four groups which were presented with both rice and background coloured were analysed by a Krus-

kall-Wallis one-way analysis of variance, using the scores for the individual chicks. Also, they were tested pairwise against each other with the Wilcoxon Rank Sum Test. This last test was also applied to a comparison between the two groups with white rice on green or red coloured background (Holländer & Wolfe, 1973).

Table 4 gives the results together with their significance levels for the groups tested simultaneously with two combinations of coloured rice and background.

Table 4. Pecking preferences of chicks exposed to two-choices combinations.

Groups	S	N	P	Groups	S	N	P
g/W	42	8	<.04	g/G	126	8	<.02
r/W	115			r/G	8		
g/B	79	8	>.05	r/R	62	8	<.02
r/B	45			g/R	21		
g/G	67	8	>.05	r/R	64	8	>.05
r/R	33			r/G	45		
g/G	73	8	>.05	g/R	73	8	<.007
g/R	37			r/G	28		

Probability levels are given for each paired comparison. Fisher's test of difference-score population symmetry about zero was used (Bradley, 1968).

From Table 4 we can see that the difference between green and red figure colour is statistically significant when presented against a white background. The similar difference on black background goes in the opposite direction, although not attaining significance. The remaining groups show the same preference order as that obtained from chicks exposed to only one stimulus combination although the statistical significance level varies a great deal.

Discussion

Looking at the groups which received only figure or background in colour (red or green), the question of whether colour preference is a general phenomenon can be answered negatively. Colour, when presented as background colour, is of no importance in directing the choice of the chicks towards the white rice (there is a slight preference for a green background although not statistically significant).

When presented as figure-colour, the impact of colour in directing the choice behaviour is significant when presented against a white background. There is a statistically significant preference for red-dyed rice grains. The preference seems to go in the opposite direction, that is for green-dyed rice exposed on black background, but does not reach significance.

Thus, the results of the experiments with only the figure or the background colour indicates that colour is an important factor in choice behaviour only when presented as object-colour. Further, the brightness of the background seems to have the opposite effects on the order of preference.

So far, our results can be directly compared to previous findings where either object or background colour have been studied. The general trend has been a preference for red or orange, green has always been found the least preferred colour (Kovach, 1971). However, our experiments could not confirm the existence of such a general trend. On the contrary, preference for coloured stimuli was found to depend both on the presentation of it as object and background. In the first case, the choice may depend on the brightness of the background.

We now look at the groups which received both coloured object and background. Although the statistical results for the one-choice and two-choice experiments do not correspond exactly,

none of them give preferences in the opposite direction. The general trend is a preference for non-contrasting combinations over contrasting ones. That is, green-dyed rice on green background and red-dyed rice on red background are preferred over combinations where rice and background colours are opposed to each other. This points to the unexpected fact that the quality of contrast vs. non-contrast is more important than the colour quality of either object or background. Furthermore, it points to the even more unexpected fact that the non-contrasting quality is superior to the contrasting one in eliciting pecking behaviour.

In each of these two categories, there is a preference for the combinations with green object colour. Even if, in the case of the two contrasting combinations, this preference could be seen as one for the red background, this interpretation is ruled out for the two non-contrasting combinations.

In summary, it can be stated that initial colour preferences in neonatal chicks is wholly dependent on the relationship between the object colour and the background colour.

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R e f e r e n c e s

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*Perceptual Determinants of Choice Behaviour
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*III. Maturational and Situational Variables in the
Early Development of Pecking Behaviour*

by Roger Sages



LUND UNIVERSITY SWEDEN

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A b s t r a c t . - Studied the pecking behaviour of 614 neonatal chicks (Ross's race) in an experimental setting involving a two-choice situation. The stimuli, rice grains which were dyed red or green, were presented on white, black or coloured backgrounds (red or green). Tests were done after different schedules of exposure where both duration and quality of the stimulus exposure was varied. The aim was to find the possible effects of maturational and specific situational variables on the pecking preferences of the chicks. The results showed that the presence of light during a period of 48 hours immediately following hatching is a necessary condition to induce a radical inversion of "initial" choice preferences (Sages, 1979). Preexposure to different combinations of object and background colours were less effective in changing choice preferences.

The early choice behaviour of the neonatal chick with regard to pecking preference seems to be determined to a considerable extent by the relationship between the colour of the choice-objects and the colour of the background on which they stand. Non-contrasting relations (green figure on green background or red figure on red background) are more effective than contrasting relations (green figure on red background or red figure on green background). Also, green is preferred to red in most combinations of figures and backgrounds, the only exception being when both colours are presented as figure colours against a white background (Sages, 1979).

These results contrast strongly with results obtained in several previous studies (Curtius, 1954; Hess, 1956; Gray, 1961; Smith and Bird, 1964; Oppenheim, Jones and Gottlieb, 1970; Kovach, 1971; Salzen, Lily and McKeown, 1971). In particular, the results on colour preferences seem to indicate a preference for red over other colours, with green usually being preferred least often. Also, stimuli contrasting in colour or brightness with the back-

ground have been found more attractive (see Sages, 1979, for further details). An explanation of discrepancies between the results obtained by the present author and those from the other studies mentioned above is needed.

A part of the explanation can lie in the difference in testing age between our study and all other ones. Our animals were tested at 12h± 6; whereas testing age in the others extended from 18h. to 30h., post-hatching.

From a theoretical point of view, however, we could ask if the method of testing at very early age is appropriate to answer the question whether a system of choice preferences is innate or learned. Behind such a method seems to lie one or several of the following assumptions:

(1) The system in question is not only phylogenetically pre-programmed, but also active immediately after hatching. It is a well known observation that the pecking behaviour can be released very early after hatching.

(2) The system works independently of preference systems coupled to other functional domains of behaviour. In principle, natural selection can have developed different types of goal-directed behaviour which are independent of one another. But it is equally conceivable that systems of behaviour which develop at a later age are partly interrelated to earlier ones.

(3) The connections between the preference system and the nervous centre in command of the motor responses are established already at the time of hatching. The motivating, organising and steering components are the main parts of every behaviour pattern. It is a common observation that the motivating part of the pecking behaviour is observable very early after the time of hatching, even before the young chick can stand on

its feet, by its observed disposition to peck at different stimuli.

Similarly, this disposition also indicates that the pecking behaviour is well organized from the start, which implies that this organisation is phylogenetically programmed.

Furthermore, the yolk sack allows the chicks to stay alive without any intake of food or water for a period of three to four days (Romanoff, 1960). It has also been proved experimentally by Cruze (1935) that the pecking accuracy is around 75% during the first day increasing slowly to 85-90% under the third day post-hatching which is around the time when the food provided by the yolk sac is coming to an end and it becomes vital for the chicks to be able to get an optimum amount of food and water. Also, early attempts by the chicks to consume food are frequently unsuccessful, as only about 15% of the pecks lead to swallowing (Breed, 1911).

In the light of the factors discussed above, a period of observation stretching over the first three days after hatching was chosen as optimal for a study of the early development of choice preferences in pecking behaviour in the present study.

The aim of this study was to look for the possible effects of both maturation and different schedules of exposure prior to testing. Thus, an attempt is made in the present study to answer the following questions: Are any of the observable changes during these three days due only to maturation? Can different kinds and amount of preexposure alter the preference order, and if so, in what ways?

Method

Subjects

During a period of several months a total of 614 domestic chicks (Ross's race), were tested for their colour preferences. Hatch-

ing temperature was 37°C and relative humidity during hatching was 85%.

Apparatus

(1) The apparatus used for pre-exposure prior to testing. 24 plywood pens with an inside area of 30cm × 18cm and a height of 25 cm were used. The pens were placed side by side. A sheet of plywood was placed under the pens.

(2) The apparatus used for testing. Plywood pens, 25cm high and having an inside area of 30cm × 36cm were placed pairwise on a plywood support in a metal frame. A mirror placed above the pens made it possible for the experimenter to make observations during testing without disturbing the chicks. Indirect lighting was obtained by two 60W neon bulbs placed outside and above the short sides of the pens. The temperature in the test room was held constant 28°C.

Stimulus Material

The stimulus material for the background consisted of coloured cardboard paper easily inserted under the pens on the plywood floor. The four colours used were red (RB-316-28), green (GY-6-8-16), black and white, according to Hasselgren's colour standards¹. The material for the stimulus figure were ordinary, elongated rice grains, white or dyed red or green with commercial food colouring to match the cardboard colours.

Procedure

After hatching in a dark incubator, the chicks were placed individually in the pens in the exposure room. The number of chicks tested each week varied due to practical reasons. All handling of the animals was done in the dim light from an electric torch. The chicks stayed in the pens for varying lengths of time and were exposed to different stimulus situations. At testing, two chicks which had received identical exposures were placed together in each one of four test pens which were observed during each test session. Each pair of chicks was tested only once. One half of each pen was covered with one combination of figure and background colours, the other half being covered with another combination.

Observation technique and scoring

The following procedure was followed: Two pens were observed simultaneously. The number of pecks to both kind of stimuli were separately registered for 15 seconds. The contribution of the two chicks in each pen was not separated. This procedure was repeated 12 times in succession. The sum of the pecks over the 12 observation periods for each pair of chicks in each pen

was calculated to form the score for them. Then, the chicks were removed, the pens cleaned, the stimulus material rearranged and new pairs of chicks introduced for testing.

Design

The general design can be divided in two parts. Part 1, shown in Table 1, has as its aim to study the question of eventual spontaneous changes in the system of choice preferences. This is obtained by observing choices after keeping the chicks during two days without exposition to coloured figure and background. Part 2, in Table 2, concerns the sensitivity of the preference system to external stimulation. The chicks are exposed to either the figure colour or the background colour or the combination of figure and background colour during varying amounts of time.

Table 1. Number of pairs of chicks tested in a two-choice situation for different combinations of figure and background colours.

Combination	N=8 for all comb. with the exception indicated	
Different figure colours against identical background colours	g/G, r/G	g/W, r/W
	g/R, r/R	g/B, r/B ⁺
Identical figure colours against different background colours	g/G, g/R	
	r/G, r/R	
Two different contrasting combinations	r/G, g/R	
Two different non-contrasting combinations	r/R, g/G	

Lower case letters refer to object colours and capital letters refer to background colours. (r, R=red, g, G=green, W=white, B=black)

⁺ N=7 for this condition only when the chicks were tested after having been kept 48h, in the dark.

The chicks were aged 12 $\pm$ 6h. when placed in the exposure pen in which they remained for a period of 48 hours; they were kept in

a dark incubator prior to that. They were thus aged 60± 6h at the time of testing. Neither coloured nor uncoloured stimulus objects were present, the chicks being exposed only to the natural colour of the plywood pens. This design was replicated with new chicks, now kept in darkness during 48 hours until testing. The design for the groups which received pre-exposure is given in Table 2.

Table 2. The different combinations of figure and background colours to which the chicks were exposed in the test situation, after pre-exposure to either a coloured figure, a coloured background or a combination of figure and background colours.

Type of pre-exposure	Test to colour combinations	Type of pre-exposure	Test to colour combinations
r	g/G, r/G	R	g/G, g/R
g	r/R, g/R	G	r/R, r/G
g/G	a. g/G, r/G	g/R	a. g/R, r/G
	b. g/G, g/R		b. g/R, r/R
	c. g/G, r/R	r/R	r/R, r/G

(N=10 for all groups in the first two cases and N=5 for all groups of the third case.)

The treatment of the chicks prior to their being placed in the exposure pens was identical to the one described in connection with Table 1. The same also holds for the explanation of the symbols. Chicks pre-exposed to a combination of object and background colours were tested after having been kept 48 hours in the exposure pens. The remaining combinations were given for a period of 4, 24 or 48 hours of exposure, each time with new individuals.

Results

We will present our data in two parts. First, the results obtained after 48 hours exposure to light without coloured object or background and those obtained after keeping the chicks 48h in the dark will be presented, compared to each other and to the data on initial choice preferences presented by Sages (1979). Second, the results obtained after different schedules of exposure to object and/or background colour will be analysed.

(1) Table 3 presents the data obtained by testing the chicks after 48 hours of dark or light exposure. Capital and lower case letters refer to figure and background colour respectively. Here, as in the following, the P-values were obtained in a series of t-tests (Winer, 1973).

Table 3. Pecking preferences of chicks exposed in two-choice combinations, after 48 hours in the dark or in light.

48 hours in the dark				48 hours in the light			
Groups.	S	N	P	Groups.	S	N	P
g/W	35	8	.19	g/W	36	8	.02
r/W	69			r/W	244		
g/B	19	7	--	g/B	97	8	.19
r/B	25			r/B	146		
g/G	114	8	.17	g/G	185	8	.22
r/G	60			r/G	269		
g/R	16	8	.008	g/R	40	8	.0009
r/R	138			r/R	374		
g/G	54	8	.16	g/G	81	8	.09
g/R	21			g/R	177		
r/G	30	8	.10	r/G	196	8	.18
r/R	61			r/R	107		
g/R	31	8	--	g/R	173	8	.13
r/G	30			r/G	287		
g/G	71	8	.29	g/G	286	8	.28
r/R	91			r/R	388		

From Table 3, we can see that the direction of preferences is the same for both conditions involving choice of coloured objects on white or black backgrounds but the differences are much larger in the condition involving preexposure to light.

Compared to the initial preferences (Sages, 1979), the trend is the same for the choices of colour on white background. However, it is reversed in the case of choices of object colour on black background. As in the case of the initial preferences, the difference is less prominent when the background is black.

We now look at the combinations involving both object and background coloured:

(A) After 48 hours in the dark, four of the six combinations show the same differences in the direction of preferences as was obtained for the initial preferences (see Table 4). In one of the two remaining cases (the combination g/R v.s. r/G), a significant initial preference for g/R is changed toward no preference for either combination. In the second case (the combination g/G v.s. r/R), the direction of preference is totally reversed, although this result does not attain significance.

(B) After 48 hours in the light, only one combination still shows the same direction of preference as was shown in the initial choice (g/R v.s. r/R). The other five combinations all have a direction of preferences which is the opposite of the initial one.

Table 4 presents the probability levels associated with a t-test of the difference between those three conditions.

Table 4. Probability levels associated to the differences between the initial preferences and the preferences after 48 hours: in the dark on the one side and the preferences after 48 hours in light.

Groups	a Initial preferences	b after 48h. dark	c after 48h. light	diff.a-c P	diff.b-c P
g/G	126	114	185		
r/G	8	60	269	.04	.13
g/R	21	16	40		
r/R	62	138	374	-	-
g/G	73	54	81		
g/R	37	21	177	.03	.04
r/G	45	30	196		
r/R	64	61	107	.13	.10
g/R	73	31	173		
r/G	28	30	287	.05	.12
g/G	67	71	286		
r/R	33	91	388	.21	-

Table 5 gives the probabilities of obtaining the distributions of probability levels in Tables 3 and 4.

Table 5. Probabilities of obtaining the distributions of probability levels from Table 3 and Table 4, (Winer, 1973).

P distribution for 48h light.	P distribution for the difference: in- initial preferences/ after 48h light	P distribution for the difference: 48h dark/48h light.
$\chi^2 = 17.90$	$\chi^2 = 26.64$	$\chi^2 = 19.36$
df = 12	df = 12	df = 12
P = .12	P = .008	P = .08

(2) Table 6 presents the data obtained by testing chicks after exposure to one of the coloured objects exposed on the plywood

floor of the pens or to one of the coloured background without any object during varying amounts of time prior to testing.

Table 6. Pecking preferences of chicks tested with two-choices combinations, after exposure to figure or background colours for 4, 24, or 48 hours.

4 hours N=10				24 hours N=10				48 hours N=10			
Groups	Exp.	S	P	Groups	Exp.	S	P	Groups	Exp.	S	P
g/G	r	120	.12	g/G	r	241	.08	g/G	r	197	.25
r/G		24		r/G		115		r/G		293	
r/R	g	139	.01	r/R	g	185	-	r/R	g	181	.18
g/R		35		g/R		186		g/R		305	
g/G	R	147	.06	g/G	R	138	.14	g/G	R	82	.09
g/R		44		g/R		230		g/R		118	
r/R	G	134	.009	r/R	G	312	.03	r/R	G	190	.33
r/G		15		r/G		91		r/G		220	

Comparing Table 6 and Table 4 it is clearly seen that an exposure time of 4 hours has no effect whatsoever on the preference order. The chicks choose the stimulus combinations in the same order as those chicks which are tested after hatching without previous exposure (the initial choice group).

Making a similar comparison after 24 hours of exposure shows the initial direction of preference to change for two groups, those being exposed to green object colour and red background colour respectively. For this last group, the preference goes in the opposite direction from the initial one. 48 hours of exposure to object or background colour results in inversion of the directions of preferences compared to the initial ones for all groups.

The probabilities of changes between conditions are given in

Table 7 and the probabilities of obtaining the probability levels of Table 6 and Table 7 are given in Table 8.

Table 7. Choice-probability levels associated with the different times of exposure to object or background colour, calculated on the data from Table 6.

4 hours condition vs. 24 hours condition	p	4 hours condition vs. 24 hours condition	p
r/R g/R	.24	g/G r/G	.12
g/G g/R	.02	r/R g/R	.05
		g/G g/R	.01
		r/R r/G	.03

Table 8. Probabilities of obtaining the probability-level distributions from Tables 6 and 7.

P distribution for the 4h con- dition	P distribution for the 48 h condition	P distribution for 4h x 24 h condition	P distribution for 4h x 48 h condition
$\chi^2 = 28.49$	$\chi^2 = 13.23$	$\chi^2 = 10.67$	$\chi^2 = 26.09$
df = 8	df = 8	df = 4	df = 8
P = .0003	P = .10	P = .03	P = .001

Table 7 shows that most of the changes in preference between the three conditions are significant.

From Table 8 we learn that the probability of obtaining the probability-level distributions from Table 4 and 5 are highly significant in all but one case.

The last conditions to be analysed were the effects of pre-ex-

posure under 48 hours to a combination of both object and background colours. The results are presented in Table 9.

Table 9. Pecking preferences of chicks exposed to combinations of object and background colours during a period of 48 hours prior to testing.

Exposed to	Test between	S	N=5	P
g/G	g/G	113	-	--
	r/G	190		
g/G	g/G	115	.	.09
	g/R	44		
g/G	g/G	177	.	.06
	r/R	31		
r/R	r/R	36	.	--
	r/G	308		
g/R	g/R	155	.	.32
	r/G	134		
g/R	g/R	115	.	.24
	r/R	24		

Table 10. Probability of obtaining the distribution of probability levels from Table 9.

$\chi^2 = 15.57$	df. = 12	P = .21
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Table 9 shows that preexposure to the combinations g/G or r/R do not change the preference for r/G as it appears after 48 hours exposure to light (see Table 3). After preexposure to g/R, the r/G combination is no longer dominant, but neither is the preexposed combination.

In all the remaining cases, the effect of the preexposure is

to change totally the direction of preference in line with the quality of the exposed combination.

D i s c u s s i o n

The most interesting aspects of the results are the radical change in the order of preferences for the four combinations of object and background colours obtained after 48 hours exposure to light, compared to the initial order of preferences. The effect of exposure to light is clearly seen when comparing with the results from the chicks kept in the dark for a comparable period prior to testing. In this last condition, four of the six combinations do not show any change of preference. In two combinations a change towards no preference in either directions can be seen. Interestingly enough, these two groups (g/R vs. r/G and g/G vs. r/R) are those which lie closest to each other according to the initial preference order, that is when tested at the age of 121 6 hours after hatching.

Hence, we have to conclude that light exposure influences the internal system directing the choice preference of the neonatal chick in pecking behaviour. The spontaneous changes observed can clearly not be due only to internal mechanisms since, in that case, similar changes should also have been observed in the chicks tested after 48 hours in darkness.

When object-colour is presented on white background, red is superior to green in eliciting pecking responses. This difference is greatest after 48 hours light exposure.

When object colour is presented on black background, red becomes superior to green only after 48 hours of exposure. In the other conditions, no preference is found. Here too, we observe a radical change only after 48 h. light, but this is restricted to choice of colour on black background.

The effects of exposure are more complex to analyse. In cases with pre-exposure to a combination of object and background colours, the pre-exposed combination always dominates the preferences when compared to the choice direction obtained after 48 hours light, except when tested against the "red object on green background" combination, that is the most preferred one after 48 hours light.

With exposure to only part of the total combination of object and background, the effect shows itself to be a progressive one, from no influence at all after 4 hours of preexposure to influence of pre-exposure to green object colour or red background colour observable after 24 hours. For three of the four groups being tested after 48h of exposure, the effects go in the same directions as those for the group tested after 48h light, hence not giving any stronger effect (almost the opposite). For the fourth group, pre-exposure to green object colour reverse the direction of preference.

The general conclusion is that the main effect observed is a spontaneous change in preferences occurring after exposure to light during 48 hours.

The effect of pre-exposure to specific stimuli, although present, seems to be less strong than this spontaneous change.

The changes can be described according to the following lines. The initial preferences were described thus (Sages, 1979): (1) A preference for non-contrasting combinations; (2) a preference for green object colour over red object colour, hence a preference for object colour over background colour; (3) dimension (1) is dominant over (2).

The preferences after exposure to light during 48 hours can be

described thus: (1) a preference for contrasting combinations over non-contrasting ones; (2) a preference for red object colour over green object colour, hence here still object colour being more important than background colour; (3) a dominance of dimension (2) over dimension (1).

We see then that this new set of dimensions directing choice behaviour can be obtained directly from the initial one by taking the exact opposite of each of its dimensions, with the exception of the general preference of object colour to background colour.

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*Perceptual Determinants
of Choice Behaviour in Neonatal Chicks*

*IV-V. Initial Preferences for colours in Following
Behaviour and Maturational and Situational
Variables affecting their Early Development*

by Roger Sages



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A b s t r a c t . - Studied the following behaviour of 1420 neonatal chicks (Ross's race) in an experimental setting involving two moving cylindrical objects painted, like the backgrounds, white, black, red or green. Tests were made according to schedules of varied duration and quality of stimulus exposure. The results showed that colour initially has differential preference values depending on its presentation as object or background colour, and that choices are also partly dependent on brightness relations between object and background. Also, ontogenetical development was characterized by an increase in the preference of the red colour and of relations of colour contrast. Preexposure to background colour had no effect on choice preferences whereas preexposure to object colour was maximally effective in totally reversing preference relations.

The following behaviour has been one of the most extensively studied forms of behaviour in ethological research literature. It was originally studied in relation to the phenomenon of imprinting. This implies a following of the parent by the young chicks of the precocial birds. According to classical ethological theory concerning the concepts of signal stimuli and innate releasers, attention has been concentrated on the differentiation of the effective components of the total stimulus configuration: in this case the parent bird. Analysis of the effective stimulus components has mostly been undertaken according to the law of heterogeneous stimulus summation. Hence, any gestalt effect has been considered as less likely.

The following behaviour can be divided into two components: "approach" and "following" proper. Both these responses have been studied, the trend in the research having been towards an increase in studies of approach responses as such. Both moving and static, two and three dimensional, coloured and uncoloured, painted and illuminated objects, static and flashing lights, have been used as stimuli. Form, colour, size and movement are the main variables that have been analysed. As our main interest in this series of

publications (see Sages, 1978, 1979, 1980) lies in the properties of colours and of possible contrast effects in the choice behaviour of the neonatal chick, only studies which are in some way pertinent to that aspect will be considered here. The results, although moving mostly in one main direction, are not wholly consistent, whereas the general findings can be summarized as follows.

Red has most often been found to be the colour most preferred and green one of the least preferred (Salzen and Sluckin, 1959; Gray, 1961; Smith and Bird, 1963; Taylor and Sluckin, 1968; Impekoven, 1969; Delius and Thompson, 1970; Kovach, 1971; Salzen, Lily and McKeown, 1971; Boltz and Drickamer, 1975). This has been observed in several different breeds of domestic chicks and even gull chicks (Impekoven, 1969).

Working with the Japanese quail (*Coturnix Coturnix*), Kovach (1974) found a higher approach tendency for green and yellow over blue and red with one day-old chicks. Red was the least preferred colour. These results were interpreted by Kovach in terms of adaptation to the natural environment. Follow-up studies carried out with two strains of quails selected for blue or red preferences, showed separately a change in the preference order between blue and red.

There are, however, some diverging results. In one of the earliest studies, Schaeffer and Hess (1958) had only a smaller choice of a yellow moving ball in a multiple-choice situation. No clear preference was obtained for any colour, red being chosen as often as green, this last colour being even slightly better than red, with chicks tested at 14 or 36 hours post-hatching. However, red was more efficient when used as a colour for imprinting. Kovach (1971) found blue to be as much and even slightly more preferred than red with domestic chicks.

Although many studies found green to be the least preferred colour, here too, there are several studies with diverging results. Boltz and Drickamer (1975) found that green followed immediately after the most preferred red colour. Delius and Thompson (1970) found the preference value of green varying in U-form with increasing intensity, although it was always less

preferred than red. Salzen and Cornell (1968) found neither a preference for red nor a negative preference for green in choices between red, green and yellow dyed chicks, both with naive chicks (which showed no preferences) and with experienced chicks (which chose the colour according to the previous experience they had received before testing). Schaeffer and Hess (1958) found equal preferences for red and green. Smith and Bird (1963) found green the least preferred colour with moving balls as stimuli, but green followed immediately after red with coloured flashing lights. All these results concern colour as object colour.

The eventual effect of the colour of the background on the colour preference of the object has not received systematic attention.

In the previously mentioned study by Boltz and Drickamer (1975) with both stationary and moving coloured objects, the background colour of the test pen was found to have no effect at all on the preference of the test objects. However, the coloured background of the pens in which the chicks were kept was a significant factor that affected colour preferences during test, but only in tests made with stationary objects as stimuli. Here too, red was found to be the most potent colour in all test situations, followed by green. Gossop (1974) obtained better following in conditions with exposure to moving figure-ground than with stationary conditions. Also, the figure-movement condition was superior to the ground-movement condition. This result is of course to be expected, as the meaning of "following" is merely to follow an object "moving" across a stationary background.

In the study by Salzen, Lily and McKeown (1971) cited above, black or white backgrounds did not modify the preference for red over green and yellow: however, brightness contrast played a role when choices were made between blue and red.

As regards brightness and intensity, some results have already been mentioned (Delius and Thompson, 1970). In this same study, red was found to be independent of intensity changes. See also the above-mentioned results of Salzen, Lily and McKeown (1971). Working with black headed gull chicks, Impekoven (1969) could rule out any explanation of the obtained preference

values of colours in terms of brightness. Weidmann (1969) obtained similar results. Kovach (1974) also found colour preferences to be independent of the intensity differences in quail chicks.

Our present aim in this study may be summarized as follows. The question of a colour preference will be reexamined, using the two colours which, according to most of the studies referred to above, seem to be on the opposite ends of the preference dimension, that is, red and green. The absolute or relative character of any possible positive or negative preference, that is, the importance of the phenomenal aspect of colour (its appearance as object- or as background-colour) will be analysed. Also, the eventual effect of contrasting or non-contrasting colour relations between the object and the background (e.g. red object exposed against red or green background) on enhancing or depleting any found positive or negative preferences will be studied. These problems will be analysed from a developmental point of view, chicks being tested at different times after hatching. The possible effects of different types of perceptual experiences, prior to testing, on colour preferences will be analysed experimentally. Finally, we will also study the possible importance of brightness in determining choice preferences.

M e t h o d

Subjects

During a period of several months a total of 1420 domestic chicks (Ross's race), were tested for their colour preferences. Hatching temperature was 37°C and relative humidity during hatching was 85%.

Apparatus

Two types of apparatus were used.

I. The apparatus used for preexposure prior to testing.

A. 24 plywood pens with an inside area of 30 cm x 18 cm and a height of 25 cm were used. The pens were placed side by side on a sheet of plywood. This arrangement was used with chicks kept for differing lengths of time in the dark or the light prior to testing. These chicks were not exposed to coloured objects or background.

B. 48 plywood pens with an inside area of 15 cm x 18 cm and a height of 25 cm were used. The pens were placed side by side on a sheet of plywood. The walls were green in half of the pens, the remaining half being red. This arrangement was used for the chicks, which prior to testing were kept for differing lengths of time in the light, without exposure to coloured or uncoloured objects (see figure 1).

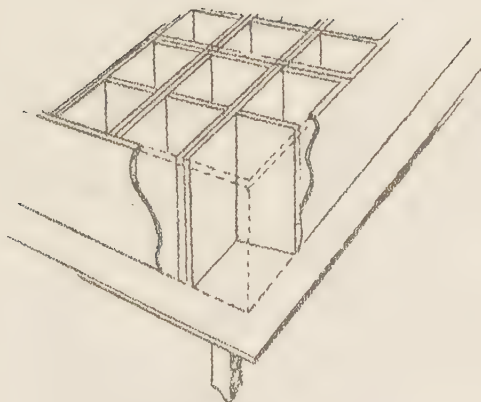


Figure 1. The preexposure apparatus used for preexposure to background colour.

C. 27 plywood pens with an inside area of 30 cm x 28 cm and a height of 25 cm were used. The pens were placed side by side on a sheet of plywood. A cylindrical object $71 \text{ cm}^2 \times 10 \text{ cm}^1$ was fixed 5 cm above the floor on a transversal axis supported 30 cm above the floor in each pen which was connected to a main axis which in turn was relayed to a motor. During preexposure the objects were kept continuously in a pendular motion at a speed of 28 revolutions per minute. Thus in each pen one object was moving along one of the short sides (see figure 2).

II. The apparatus used for testing.

One plywood pen, 25 cm high and 100 cm x 40 cm, was placed on a plywood support within a metal frame. A mirror placed above the pen made it possible for the experimenter to make observations during testing without disturbing the chicks. Indirect lighting was obtained by two 60 W neon bulbs placed outside and above the short sides of the pen. The same stimulus object as that described above (cf. I.C.) was used. However, in the test pen, two of these objects were presented simultaneously, each one moving pendularly across each of the short sides of the pen at a distance of 6.5 cm from it, 5 cm above the floor. Both

1) Research conducted by Schulman, Hale & Graves (1970) found that a size of 10 to 20 cm was optimal in releasing the following response in young chicks.

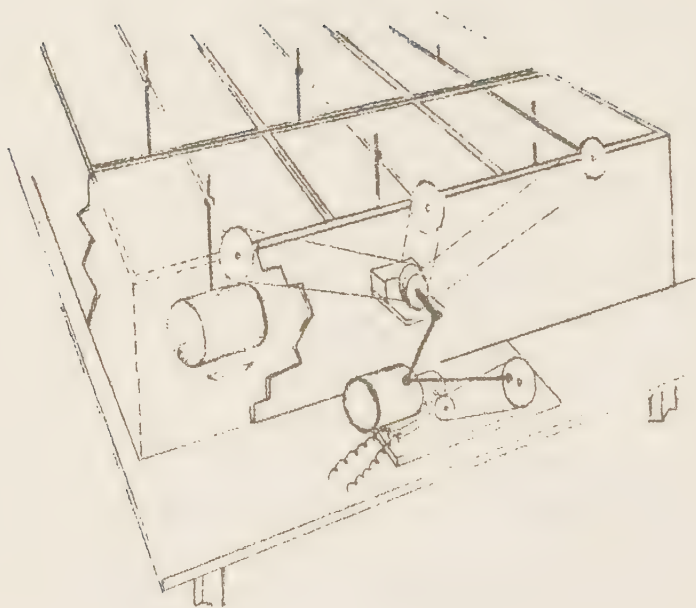


Figure 2. The apparatus used for preexposure to object colour.

objects were suspended from the same axis that runs along the long sides of the pen and were connected to a motor inducing the same speed as during the preexposure, that is, 28 revolutions per minute (see figure 3).

The temperature in the preexposure room was 28°C and 21°C in the test room¹⁾

Stimulus material

The colours used were red (RB-37-16-28)²⁾, green (GY-6-8-16), black and white. The first two colours were painted on the objects used both for pre-exposure and testing. As stated previously, green and red colours were also used as colour for the walls of the pens used for preexposure. Black and white were never used in preexposure, neither as object nor as background

1) Fischer (1970) found a temperature fall from ca 28°C to 20-22°C between the exposure room and the test room to be maximally effective in eliciting the following behaviour in the young chick.

2) Hesselgren's colour standards.

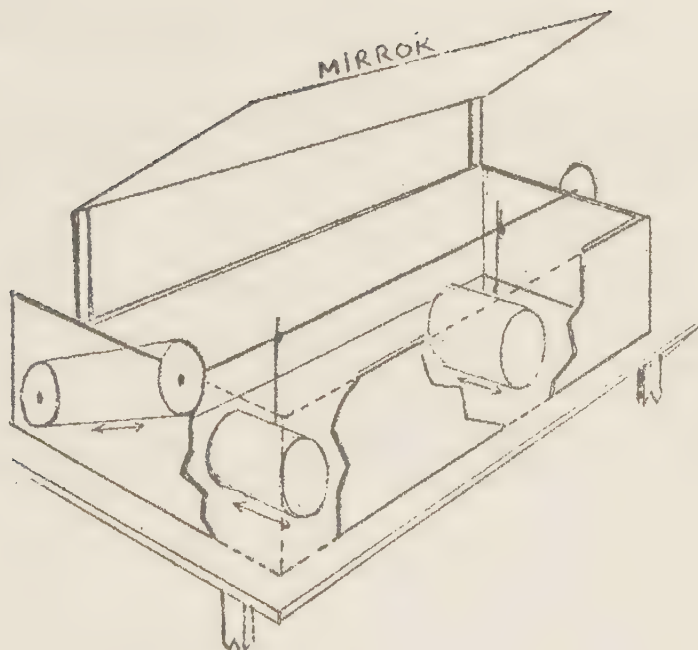


Figure 3. The apparatus used for testing.

colours. The walls of the test pens could be easily covered with removable cardboard paper, in one of the above-stated colours. The two halves of the test pen could be covered separately, allowing the different combinations of background colours to be presented.

Procedure

After hatching in a dark incubator, the chicks were placed individually in the exposure room. All handling of the animals was performed in the dim light of an electric torch. The chicks stayed in the pens for varying periods of time and were exposed in different stimulus situations: then, at the appropriate time, they were placed exactly in the middle of the testing pen, facing one of the long sides. Each chick was tested individually and only once.

Observation technique and scoring

The following procedure was observed:

As soon as a chick was placed in the test pen, an observation period of five minutes began. Recording of the time during which the chick stayed in each of the two choice regions (see figure 3), was made separately.

The score for each individual consisted of the total length of time it had stayed near respective objects. Hence, for example, a chick could obtain the score of 210 seconds near one object, and 75 seconds near the other, stopping at almost equal distance from the two objects during 15 seconds. After the 5 minutes observation period, the chick was removed, the pen cleaned, the stimulus material rearranged and a new individual was introduced for testing.

Design

The general design can be divided into two parts. Part 1, depicted in Tables 1 and 2, has as its aim to study, first, the initial preferences of the chicks, but also, possible trends in these preferences. This is obtained by observing choices after keeping the chicks during differing periods of time without exposure to coloured or uncoloured objects or to coloured backgrounds. Part 2, depicted in Table 3, has, as its aim, the question of the sensitivity of the preference system to external stimulation. This is obtained by exposing the chicks to either the coloured object or the coloured background during varying lengths of time prior to testing.

Table 1. Number of chicks tested in a two-choice situation for different combinations of object and background colours.

Combination comparison	N = 12 for all combinations		
Different object colours against identical background colours	g/G, r/G	g/W, r/W	w/G, b/G
	g/R, r/R	g/B, r/B	w/R, b/R
Identical object colours against different background colours	g/G, g/R	g/W, g/B	w/G, w/R
	r/G, r/R	r/W, r/B	b/G, b/R
Contrasting and non-contrasting combinations of coloured object and background	r/G, g/R	r/R, g/G	
Other combinations with differ- ent object and background colours	g/W, r/B	w/G, b/R	
	g/B, r/W	w/R, b/G	

Lower case letters refer to object colours and capital letters refer to background colours. (r,R=red, g,G=green, w,W=white, b,B=black).

The design from Table 1 was applied to different groups of chicks after differing periods of time as follows from Table 2.

Table 2. Time in hours prior to testing, during which the chicks were kept in isolation.

Kept in the dark before testing			Kept in the light before testing		
6	24	48	6	24	48

The design of Part 2 is shown in Table 3. It was applied twice, once after 24 hours and once after 48 hours exposure prior to testing. Here too the chicks were 6 to 12 hours old and kept in the dark before preexposure. Of course, in all cases new individuals were used as already stated.

Table 3. The different combinations of object and background colours to which the chicks were exposed in the test situation, after preexposure to either a coloured object or a coloured background.

Preexposure to background colour	Colour combinations used during testing	Preexposure to object colour	Colour combinations used during testing
G N=11,10	g/G,r/R	g N=6,4	g/G,r/R
G N=11,10	g/G,g/R	g N=5,4	g/G,r/G
R N=22,20	g/R,r/G	r N=6,4	r/R,g/R
		r N=5,5	g/R,r/G

The two numbers after each N give the number of chicks tested in the two conditions, i.e., 24 and 48 hours.

The treatment of the chicks prior to their being placed in the exposure pens was identical with the one described in connection with Part 1. The same also holds for the explanation of the symbols.

Results

The results will be presented in two parts. Part one contains the data obtained by testing the chicks in a two-choice situation after differing times of exposure (cf. Design). Part two contains the data obtained by testing chicks in the two-choice situation after differing times of pre-exposure to either object or background colour.

Part 1. A. Table 4 presents the data obtained with black or white objects and coloured backgrounds. Tests were made after periods of 6, 24, or 48 hours in the dark or in light, each time with new individuals. Student's t-test of the difference of the means between two dependent populations was used, applied on the raw scores obtained from each chick. It was used for all comparisons presented in Tables 4, 6, 8, 10 and 11 (Winer, 1973). The figures given in the tables are the sums of the raw scores obtained from each chick in each comparison group.

Table 4. Total length of time spent by the chicks, in minutes and seconds, near either part of the stimulus combinations, together with the level of probability associated to the differences (N = 12 for all groups).

Test to	A: initial		B: 24 hours		C: 48 hours	
	Dark P	Light P	Dark P	Light P	Dark P	Light P
a: w/G	0	4	12.05	0.45	12.45	15.20
b/G	14.45 .005	19.50 .01	12.45 .48	21.45 .006	17.35 .31	13.20 .19
b: w/R	26.25	13.20	23.40	6.40	14.10	18.15
b/R	1.45 .003	8.15 .29	2.20 .001	18.05 .08	11.50 .36	9 .19
c: w/G	6.55	8.05	10.55	4.35	4.05	1.40
w/R	10.30 .33	27.25 .04	7.10 .32	21.25 .02	18.20 .02	29.05 .0002
d: b/G	20.15	4.25	16.10	7.30	13.30	2.30
b/R	0.15 .004	27.05 .009	11.35 .29	7.15 .48	14.55 .44	18.05 .02
e: w/G	18.35	2.55	6.45	0.20	5.40	6.10
b/R	8.55 .18	24.15 .004	21.05 .08	13.15 .02	12.55 .15	25.10 .02
f: w/R	19.25	16.50	7.15	4.30	13.30	21.55
b/G	15.25 .37	13.35 .53	16.30 .14	10.55 .14	11.35 .41	9.45 .22

From Table 4 we obtain the following observations; the rows (c) and (d) indicate most clearly the possible preferences for green or red background colour, since the object in each two-choice combination is either white or black. Chicks preexposed to light have a clear preference for the red coloured background already from the first day. Chicks kept in the dark prior to testing have a preference for red only on the third day with white objects: with black objects, there is an initial preference for the green

coloured background which however lasts for only the first day. (see Fig. 4).

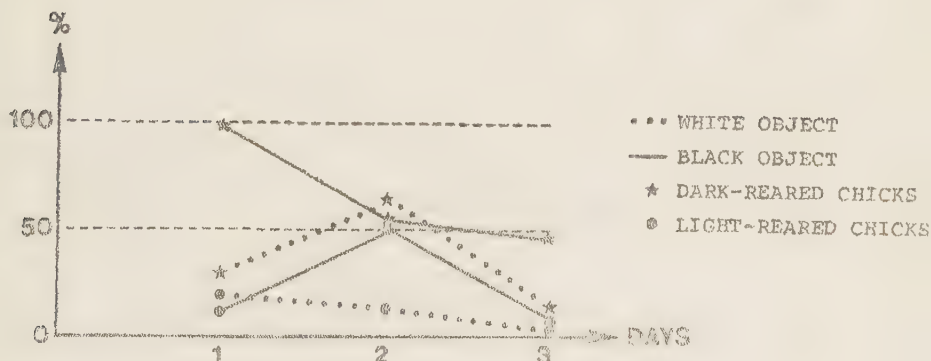


Figure 4. Percentual representation of choice preferences for groups in row (c) and (d) of Table 4. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green backgrounds.

Rows (e) and (f) also contain choices between red and green backgrounds, but with object of opposite brightness in each row. Chicks preexposed to light have a clear preference for the red background from the first day onwards, but only those tested with the w/G, b/R combination. Chicks kept in the dark do not have any clear preference except, perhaps, for red on the second day for those tested with the w/G, b/R combination (see Fig. 5).



Figure 5. Percentual representation of choice preferences for groups in row (e) and (f) of Table 4. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green backgrounds.

The first two rows give an indication of a possible preference in brightness relations. Black objects are preferred to white on the first day for both dark and light-reared chicks, when exposed on green backgrounds. This preference is present on the second day for light-reared chicks. When exposed on red backgrounds, only light-reared chicks show this tendency on the second day. Dark-reared chicks have a strong preference for the white object during the first two days. (see Fig. 6).

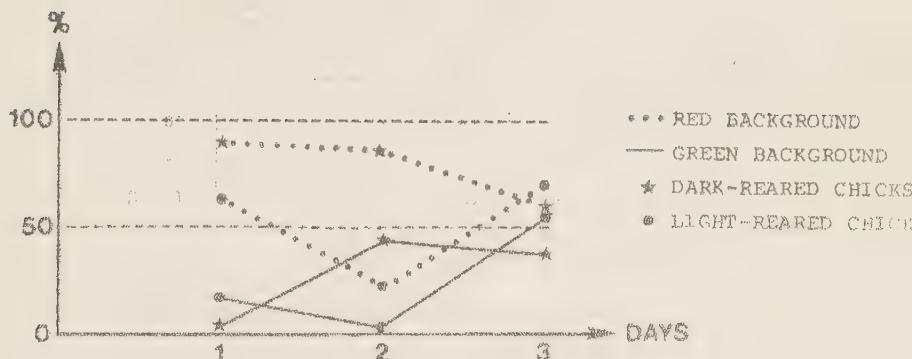


Figure 6. Percentual representation of choice preferences for groups in row (a) and (b) of Table 4. 0 to 50% indicates a dominance for black objects and 50 to 100% a dominance for white objects.

Table 5 gives the probabilities of obtaining the distributions of probabilities in Table 4. The calculation, made on the assumption of no preference for either colour, is based on cells from the rows (c), (d), (e) and (f). The calculation of the χ^2 value was repeated for each column in turn, giving a value for all conditions of dark-light and exposure durations.

From Table 5, we read a clear indication of preference for red with light-reared chicks. There is evidence for a preference for green with dark-reared chicks. This preference disappears on the second day, changing towards a preference for red on the third day.

Table 5. Probabilities of obtaining the distributions of probability levels from Table 4.

A: initial		B: 24 hours		C: 48 hours	
Dark	Light	Dark	Light	Dark	Light
pref. for green	pref. for red	pref. for green	pref. for red	pref. for red	pref. for red
$\chi^2=14.47$	$\chi^2=28.17$	$\chi^2=8.68$	$\chi^2=15.64$	$\chi^2=15.04$	$\chi^2=35.71$
df.= 8	df.= 8	df.= 8	df.= 8	df.= 8	df.= 8
P = .07	P = .0004	P = .36	P = .04	P = .05	P = .00001

B. Table 6 presents the results obtained with red- or green-coloured objects on white or black backgrounds. Tests were made after periods of 6, 24 or 48 hours in dark or light, each time with new individuals.

Table 6. Total length of time spent by the chicks, in minutes and seconds, near either part of the stimulus combinations, together with the level of probability associated with the differences. (N = 12 for all groups).

Test to	A: initial		B: 24 hours		C: 48 hours	
	Dark P	Light P	Dark P	Light P	Dark P	Light P
d: g/W	9.40	1.40	23.05	13.50	13.40	12.15
g/B	10.35	19.10	2.50	8.45	13.35	15
r/W	15.40	19.10	26.50	25.45	26.15	20.50
r/B	8.30	11.35	5.00	4.30	8.25	2.40
c: g/W	7.25	6.10	16.20	2.15	6.05	3
r/W	16.55	22.35	16.10	39.50	26.45	34
d: g/B	4.20	0	5.40	11.30	7.25	0.25
r/B	19.55	26.40	18	21.25	14.30	16.35
e: g/W	5.55	5.15	8.50	3.25	15.05	11
r/B	21.20	20.25	16.20	29.10	13.00	13.25
f: g/B	5.30	0.15	0.15	0.35	4.55	12.50
r/W	25.10	21.15	38.05	29.30	25.25	21.30

From Table 6 we obtain the following observations. Here too, the rows (c) and (d) indicate the possible preferences for green or red as object colours, since the background in each two-choice combination is either white or black. Chicks preexposed to light have a clear preference for the red coloured object already from the first day. Chicks kept in the dark, prior to testing, show the same preference only on the second or third day, for those tested on black or white backgrounds respectively (see Fig. 7).

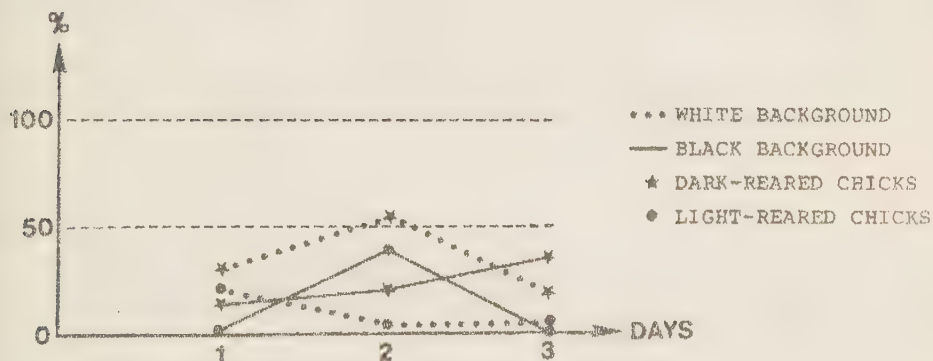


Figure 7. Percentual representation of choice preferences for groups in row (c) and (d) of Table 6. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green objects.

Rows (e) and (f) also present choices between red and green object colours, but here with backgrounds of opposite brightness. Chicks preexposed to light have a clear preference for the red object with all combinations except on the third day. Chicks kept in the dark, prior to testing, show the same preference with the exception of the second and third days for those tested with the g/W, r/B combination. (see Fig. 8).



Figure 8. Percentual representation of choice preferences for groups in row (e) and (f) of Table 6. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green objects.

The first two rows give an indication of a possible preference in brightness relations. Chicks preexposed to light prefer the black background with green objects on the first day, whereas a preference for a white background is shown with red coloured objects on the second day. Chicks kept in the dark have preferences for the white background on the second day for both combinations and on the third day with red-coloured objects only. (see Fig. 9).

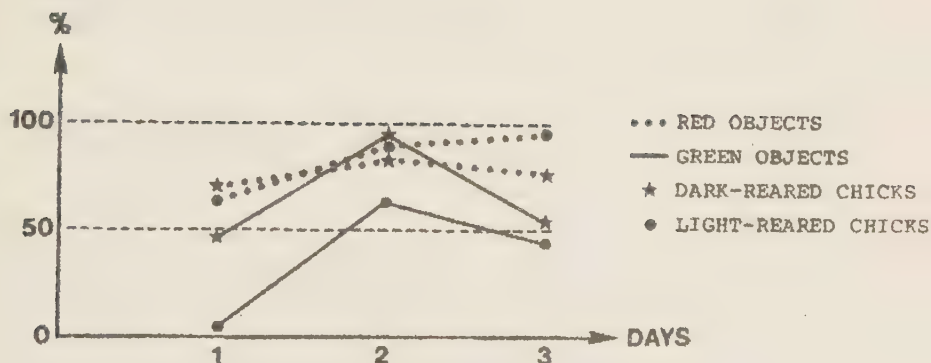


Figure 9. Percentual representation of choice preferences for groups in row (a) and (b) of Table 6. 0 to 50% indicates a dominance for black and 50 to 100% a dominance for white backgrounds.

Table 7 gives the probabilities of obtaining the distributions of probability levels in Table 6. Here too, as for Table 5, the calculation is made on the assumption of no preference for either colour and is based on cells from the rows (c), (d), (e) and (f).

Table 7. Probabilities of obtaining the distributions of probability levels from Table 6.

A: initial		B: 24 hours		C: 48 hours	
Dark	Light	Dark	Light	Dark	Light
Pref. for red	Pref. for red	Pref. for red	Pref. for red	Pref. for red	Pref. for red
$\chi^2=23.24$	$\chi^2=34.06$	$\chi^2=33.06$	$\chi^2=51.78$	$\chi^2=23.49$	$\chi^2=27.93$
df.= 8	df.= 8	df.= 8	df.= 8	df.= 8	df.= 8
P = .003	P = .00003	P = .00005	P = .00000007	P = .002	P = .0004

From Table 7, we read of a very strong preference for red on all three days and over all conditions of rearing prior to testing.

C. Table 8 presents the results obtained with red and green as both object and background colours. Tests were made after periods of 6, 24 or 48 hours in darkness or light, each time with new individuals.

Table 8. Total length of time spent by the chicks, in minutes and seconds, near either part of the stimulus combinations, together with the level of probability associated with the differences. (N = 12 for all groups).

Test to	A: initial		B: 24 hours		C: 48 hours	
	Dark P	Light P	Dark P	Light P	Dark P	Light P
a:	g/G 3.50 .002	4.55 .006	13.15 .20	0 .00009	8.25 .29	3.30 .0002
	g/R 33.30	36.25	23.05	28.30	14.00	41.55
b:	r/G 7.30 .08	14.40 .37	11.30 .13	20.45 .02	23.45 .16	16.30 .47
	r/R 20.10	17.45	5.00	6.10	16.00	15.50
c:	g/G 5.50 .23	3.15 .01	1.05 .006	0 .0009	6.00 .12	5.10 .02
	r/G 11.15	18.35	19.00	32.25	15.45	21.05
d:	g/R 12.35 .19	7.40 .19	16.20 .49	25.20 .01	13.45 .22	30.55 .02
	r/R 7.00	17.50	16.10	4.55	21.35	9.35
e:	g/G 0.30 .001	1.30 .005	3.45 .07	2.30 .008	0.05 .0007	7.25 .06
	r/R 33.15	22.50	16.15	19.15	25.55	23.40
f:	g/R 3.10 .002	17.20 .30	13.00 .43	10.40 .43	16.05 .34	5.30 .38
	r/G 32.35	12.05	11.25	12.00	13.15	7.30

The results of Table 8 are more complicated to read as both the colour dimension and the contrast dimension are intermingled here with each other. For example, in row (c), the combinations can be described as offering a choice of object colour on identical background colour, but it can also be described as a choice between a contrasting and a non-contrasting combination. We can begin by looking at row (e). It offers a choice between two non-contrasting combinations, hence a choice between red or green combinations. The r/R combination is clearly preferred over all other conditions.

Similarly, row (f) offers a choice between two contrasting combinations. No preference for either can be observed except in the case of dark-reared chicks during the first day, where a preference for the r/G combination is observed. (see Fig. 10).

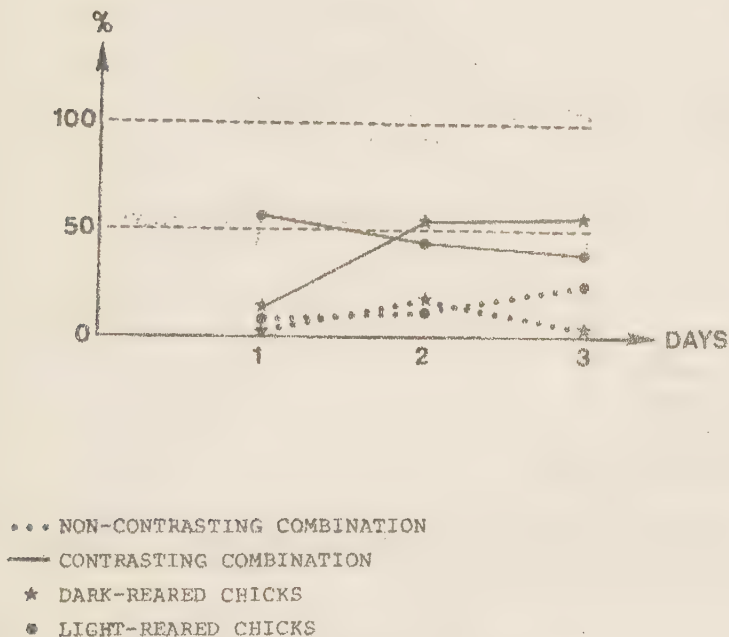
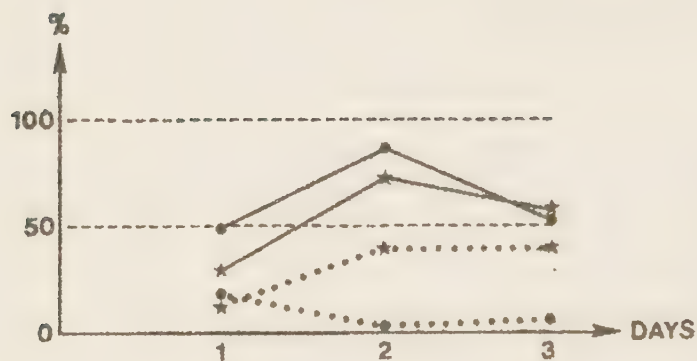


Figure 10. Percentual representation of choice preferences for groups in row (e) and (f) of Table 8. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green objects.

Rows (a) and (b) offer choices between colours of backgrounds. Chicks pre-exposed to light have a clear preference for the combinations contrasting in colour except on the first and third day with the r/G, r/R combinations. Chicks kept in the dark have preferences only on the first day, for g/R with the g/R, g/G combination and for r/R with the r/G, r/R combination. (see Fig. 11).



- ... GREEN OBJECTS
- RED OBJECTS
- ★ DARK-REARED CHICKS
- LIGHT-REARED CHICKS

Figure 11. Percentual representation of choice preferences for groups in row (a) and (b) of Table 8. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green backgrounds.

Rows (c) and (d) present choices between colours of objects. Chicks pre-exposed to light have a clear preference for the combinations contrasting in colour except on the first day with the g/R, r/R combination. Chicks kept in the dark, prior to testing, have a clear preference for the contrasting combination only with the g/G, r/G combination on the second day (see Fig. 12).

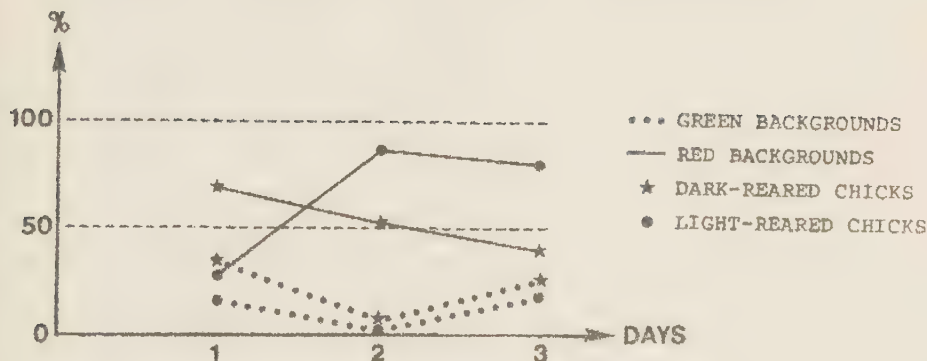


Figure 12. Percentual representation of choice preferences for groups in row (c) and (d) of Table 8. 0 to 50% indicates a dominance for red and 50 to 100% a dominance for green objects.

Table 9 gives the probabilities of obtaining the distributions of probability levels in Table 8. Here, two different types of calculations were made. The first one is made on the assumption of no preference for either contrasting or non-contrasting combinations. The calculations are based on the cells from rows (a), (b), (c) and (d). The second type of calculation is based on the assumption that there is no preference for any colour. Here, the calculations are based on all rows with the exception of row (f) which has each colour as object colour in one combination and as background colour in the other one. As an example, row (d) has the two combinations g/R and r/R. As the red colour appears both as object and background colour, it is weighted more in favour of red than g/R: hence, a preference is counted as going in favour of red if the r/R combination is preferred to

the g/R one.

Table 9. Probabilities of obtaining the distributions of probability levels from Table 8.

I. Preferences in favour of contrasting combinations. Df. = 8					
A: initial		B: 24 hours		C: 48 hours	
Dark	Light	Dark	Light	Dark	Light
$\chi^2 = 18.69$	$\chi^2 = 24.04$	$\chi^2 = 18.95$	$\chi^2 = 49.69$	$\chi^2 = 10.38$	$\chi^2 = 34.19$
P = .01	P = .002	P = .01	P = .00000004	P = .23	P = .00003

II. Preferences in favour of the red colour. Df. = 10					
A: initial		B: 24 hours		C: 48 hours	
Dark	Light	Dark	Light	Dark	Light
$\chi^2 = 34.23$	$\chi^2 = 39.95$	$\chi^2 = 17.76$	$\chi^2 = 42.31$	$\chi^2 = 24.27$	$\chi^2 = 30.48$
P = .0001	P = .00001	P = .04	P = .000006	P = .006	P = .007

We see from Table 9 that the preferences are very strong both in favour of contrasting combinations and in favour of the red colour with only one exception.

Part II. A. Table 10 presents the data obtained in two-choice tests with the chicks having been preexposed to coloured backgrounds during 24 or 48 hours after hatching.

Table 10. Total length of time, in minutes and seconds, spent by the chicks near either part of the stimulus combinations, together with the level of probability associated with the differences.

Type of preexposure	Type of test combination	Duration of preexposure 24 h	Duration of preexposure 48 h
a. G	g/G	8.05	14.50
	r/R	38.15 N=11 P=.01	23.55 N=10 P=.20
b. G	g/G	12.55	4.00
	g/R	25.50 N=11 P=.09	21.05 N=10 P=.04
c. R	g/R	38.50	28.35
	r/G	42.25 N=22 ----	29.55 N=20 ----

In the first two cases, preexposure to a green coloured background has no effect in changing the direction of preference towards the less favoured g/G combination. We saw from Table 8 that there is no evidence for any preference for either the g/R or the r/G combination on the second and third days. From Table 10, we read that preexposure to a red background has no effect whatsoever affecting this state of fact.

B. Table 11 gives the results concerning preferences after preexposure to coloured objects only.

In the second column, the second combination listed for each cell is the one of the two being preferred after periods of time equivalent to the durations of preexposure (see Table 8). Keeping that in mind, it can be seen that for the first three cases (rows a, b, c) preexposure to object colour changes more or less strongly the direction of preference. This is not the case for the results of the fourth row where preexposure has no effect at all on the choice preferences.

Table 11. Total length of time, in minutes and seconds, spent by the chicks near either part of the stimulus combinations, together with the level of probability associated with the difference.

Type of preexposure	Type of test combinations	Duration of preexposure 24 h	Duration of preexposure 48 h
a. g	g/G	17.40 N=6 P=.27	16.20 N=4 P=.0007
	r/R	10.25	0
b. g	g/G	18.55 N=5 P=.004	8.25 N=4 P=.36
	r/G	3.10	5.15
c. r	r/R	19.45 N=6 P=.002	12.15 N=4 P=.03
	g/R	0.20	3.15
d. r	g/R	10.00 N=5 P=---	12.55 N=5 P=.28
	r/G	10.10	7.55

General summary of the results

A. Initial preferences.

I. Preference of colour as background colour.

The results indicate that there is no clear-cut preference for red or green as background colours. The question of an initial preference should be answered by looking at the results from the dark-reared chicks on the first day. These results are ambiguous as a preference for green is shown only with black objects, no preference being shown with white objects. In the condition with white and black objects, no preference for either colour can be observed. Hence green seems to be preferred to red, but the relationships between object brightness and background colour also plays a part in directing choices. The tests of preferences between object brightness indicate a preference for black when presented on a green background, and for white on a red background. This contributes to the explanation of the above-mentioned lack of preference.

II. Preference of colour as object colour.

Here the situation is much easier. Already on the first day, there is a

clear preference for the red object colour. As for brightness preference, the white and black backgrounds are equally preferred when presented with two objects of the same colour.

III. Preference of colour when combined as object and background colours.

The comparison between the non-contrasting stimuli give a clear preference for red, the comparison between the two contrasting stimuli give a slight preference for the r/G combination. This can be interpreted either as a preference for red object colour or for green background colour. From the two previous sections, both these characteristics can be expected to contribute to the preference observed. In three of the four remaining cases, the contrasting combination is preferred to the non-contrasting one.

B. The Development of initial preferences.

I. The development of preference of colour as background colour.

- a. The development for dark-reared chicks: The slight preference for green observed on the first day changes towards a preference for red on the third day. No brightness preference is evident on the third day.
- b. The development for light-reared chicks: The marked initial preference for red lasts on the following days.

II. The development of preference of colour as object colour.

- a. The development for dark-reared chicks: The observed initial preference for red is also evident on the following days. But different test combinations do not give consistent results for all all three days, although in each case, the χ^2 analysis gives a clear preference for red. In three of the four cases during the second and third day, there is a clear preference for choice of an object exposed against white background.
- b. The development for light-reared chicks: Here, too the initial preference for red is evident on the following days. But although on the first day the preferences in all four test combinations offering choices between colours have very strong probabilities of occurrences, only three of them on the second day and two on the third day give rise to differences in choices. There is also a change from black towards white backgrounds during the three days.

III. The development of preference of colour when exposed both as object and background colour.

- a. The development for dark-reared chicks: The overall χ^2 analysis gives marked preference for red on all three days. The same can be established for the preference regarding contrasting combinations, which disappears only on the third day. No clear order of preference can be established on the third day between the four combinations of object and background colours with the exception of the g/G combination, which is still clearly less preferred than any of the other ones.
- b. The development for light-reared chicks: The initial preferences for red colour and contrasting combinations are also observed on the following days, most strongly on the second day. As for the dark-reared chicks, g/G is the least chosen combination on all three days. The lack of preference between the two contrasting combinations is evident on all days. The non-contrasting red combination is least preferred on day two except when compared to the g/G combination. Here too, no clear order of preference can be established on the third day.

IV. The general conclusion concerning the development of colour preference.

As object colour, the preference for red remains during the three days. For background colour, there is a marked increase in strength of preference for red as especially evidenced by the change from green to red with dark-reared chicks. All initial preferences of brightness disappear on the third day as long as object brightness is concerned. For background brightness, there is a development towards a preference for white. Both the red and the contrast preferences diminish during the three days, for dark-reared chicks. The opposite is true for light-reared chicks.

C. The effects of preexposure before testing on the initial preferences.

The results show without ambiguities that preexposure to the colour of backgrounds have no effect in changing established preferences. On the other hand, exposure to the colour of the object is very effective in changing these preferences.

Discussion

The first point to be studied was the relative importance of colour as object or background colour in directing choice behaviour. The results indicate that the effects of object colour are not dissociable from the background colour and the reverse is also true. Hence, the independent values of the object colours obtained with black or white backgrounds and of the background colours obtained with black or white objects are not simply additive, but interact with each other. This result is not to be expected from the law of heterogeneous stimulus summation. Also, it runs contrary to the results obtained by Boltz and Drickamer (1975) who found no effects of background colour in the testing pen.

The marked initial preference for the red-coloured object agrees well with an evolutionary point of view interpreting the preference for red in following behaviour as a result of natural selection pressure due to the red coloured patch on the back of the head of the ancestral form of today's domestic chick (*Gallus bankiva*), whose function is supposed to be that of an innate releaser. In this case, an inborn preference for red would be expected for the following behaviour.

The initial preference for green background colour, although not as pronounced as the preference for red object colour, indicates that, initially at least, the two preferences are controlled by quite different processes, and as such are the results of different selection mechanisms.

The very early change in preference of background colour from green to red can be due to several reasons (an internal change in the system controlling it, a subordination of it to the system controlling object colour) but, evidently, more research is needed to answer this question.

On the other hand, the preference for the red coloured object remains during all three days, as would be expected from the evolutionary theory as referred to above.

The second part of the study indicated very clearly that exposure to coloured backgrounds does not alter the choice preferences of the chicks.

Exposure to coloured objects alter radically their choice preferences. These findings are in agreement with those of Gossop (1974). Here we have a situation analogous to the classical imprinting experiments where a moving object is a most potent stimulus to which the animal becomes imprinted. But our situation here is more complex to analyse and interpret.

First, although an exposure to green will orient the chicks towards a preference for it, there is an inborn preference for red which remains unaltered during at least the first three days. We then have a system which comprises paradoxically both an inborn preference and a great sensitivity to external stimulation.

Secondly, the inborn preference for green-coloured backgrounds changes during the first two days by an internal process and is, during this time at least, totally insensitive to external stimulation. It is interesting to note these differences between the systems governing preferences for object and background colours in view of background preferences being less important than object preferences in a following behaviour for obvious reasons.

Also, the brightness of the background had an effect. Red was preferred on a white rather than on a black background; no such effect was recorded for green. When white or black objects were presented against coloured backgrounds, differential choice preferences were observed. These findings contradict those obtained by Salzen, Lily and McKeown (1971) and Delius and Thompson (1970).

Lastly, the relation of colour contrast between the object and the background was important already from the first day, contrasting combinations being on the whole preferred to non-contrasting ones.

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